THE SUBTRIBES AND GENERA OF THE TRIBE BROSCINI (COLEOPTERA: CARABIDAE): CLADISTIC ANALYSIS, TAXONOMIC TREATMENT, AND BIOGEOGRAPHICAL CONSIDERATIONS

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ABSTRACT

Phylogenetic relationships of the genera of the tribe Broscini (Carabidae) are postulated based on cladistic methods. Seventy-three morphological characters were examined in 88 species, arranged in 41 genera and subgenera, and with the related tribes Melaenini and Apotomini as outgroups. In all the obtained cladograms, the genera are grouped in five clades recognized as the basis for a new subtribal classification: the Oriental-Palearctic-Neotropical Axonyina, new subtribe (type genus, *Axonya* Andrewes) with 3 genera; the Holarctic-Oriental subtribe Broscina (type genus *Broscus* Panzer) with 9 genera; the south temperate Australian-Neotropical Nothobroscina new subtribe (type genus *Nothobroscus* Roig-Juñent and Ball) with 10 genera; the south temperate Neotropical Barypina (type genus *Barypus* Dejean) with 2 genera; and the south temperate Australian-Neotropical Creobiina (type genus *Creobius* Guérin-Méneville) with 11 genera. Species groups within diverse genera *Barypus*, *Eurylychnus* Bates, and *Promecoderus* Dejean were treated as terminal units to test monophyly of these genera. Results of the analysis show that only *Promecoderus* is not monophyletic, as presently structured. Keys and diagnoses are provided for the genera of Broscini, and all taxonomically important structures are illustrated. Genital features of males and females are described for the first time for several genera. The barypine genus *Microbarypus*, with its type species *M. silvicola* (type locality Alto Queulat, Aisén, Chile) is described as new. The species *Percosoma concolor* Sloane, *P. substriatum* Moore, and *P. montanum* Castelnau are transferred to the genus *Chylnus*. Type species are designated for *Adotela* Castelnau (*Adotela concolor* Castelnau), *Gnathoxys* Westwood (*Gnathoxys granularis* Westwood), and *Cerotalis* Castelnau (*Cerotalis substriata* Castelnau). The four main biogeographical hypotheses proposed to explain Broscini distribution are discussed. Recent discovery of new Neotropical genera, as *Nothobroscus* Roig-Juñent and Ball and *Rawlinsius* Davidson and Ball, together with the phylogeny of Broscini, lead to a different biogeographic hypothesis. Broscini can be considered a Pangaeic tribe originating in lower Jurassic times when there was a land connection between South America and North America on the Pacific margin. In broad terms, the biogeographic pattern of Broscini may be explained by the current hypothesis of the breakup of Pangaea.

INTRODUCTION

The carabid tribe Broscini is a moderately diverse and structurally divergent group with about 267 species in 36 genera (14 monospecific). The species of Broscini present a worldwide distribution in areas of temperate and subarctic conditions both north and south of the tropics, except for a genus from Mexico (Davidson and Ball, 1998). Some of the northern species are winged, whereas the southern species have atrophied wings. Most species and genera occur in the Southern Hemisphere, distributed in three main areas: southern Australia plus Tasmania, New Zealand, and southern South America.

Successive classifications of Broscini have been proposed using previously unstudied characters. Thus, Jeannel (1941) pointed out the importance of the internal structures of male genitalia and divided the tribe into three subtribes. Ball (1956) revealed the significance of internal sac sclerites, supporting Jeannel's subtribal classification; but Ball proposed a different arrangement of genera. In any case, classifications based on a single system hardly reflect natural relationships.

Many of the characters used in the present analysis are based on similarities and differences of internal structures. Among these, the male genitalia (Jeannel, 1955) and the female reproductive tract (Deuve, 1993) have been the subject of extensive comparative studies in Carabidae. In addition, several characters traditionally held to be of taxonomic importance, like most of those used by Deuve (1993), were also included in this study.

Here, I analyze the cladistic relationships among Broscini genera, using characters from both external morphology and female and male genitalic structures.

MATERIAL AND METHODS

The studied material was provided by following institutions and Curators:

AMNH American Museum of Natural History, New York, New York, USA (Lee H. Herman Jr.)

ANIC	Australian National Insect Collection, CSIRO, Canberra, Australia (T. A. Weir)
CM	The Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA (Robert L. Davidson)
CUIC	Cornell University Insect Collections, Ithaca, New York, USA (James K. Liebherr)
IADIZA	Instituto Argentino de Investigaciones de Zonas Aridas, Mendoza, Argentina
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (Philip Perkins)
MLPA	Museo de La Plata, La Plata, Argentina (Juan Schnack)
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain (Isabel Izquierdo)
NSDU	North Dakota State University, Fargo, USA (Allan Ashworth)
UASM	Strickland Entomological Museum, National Museum, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada (George E. Ball)
USNM	Smithsonian Institution, Washington, D.C., USA (Terry Erwin)

Drawings were made with camera lucida. Scale bars represent 1 mm.

TAXA: For the present study I examined species representatives of all the genera and subgenera recognized in catalogs or systematic studies, with the exception of some uncommon taxa, such as *Bountya*, *Ebertius*, *Rawlinsius,* and *Sinobrosculus* for which material was not available. The genera *Bountya* and *Rawlinsius* could be included in the analysis because the information on their characters is quite complete in the original descriptions (Townsend, 1971; Davidson and Ball, 1998), but *Sinobrosculus* and *Ebertius* were not included because information was limited. A total of 88 species were examined (species with an asterisk in appendix 1). Because specimens of one sex were not available for the genera *Broscodes*, *Axonya*, and *Eobroscus,* their characters were coded as missing in the analysis. The type species of each genus was examined. The number of species studied depended on the size and diversity of the respective genera. For genera with little morphological variation, such as *Mecodema*, relatively few species were examined. A larger number of species was examined for genera showing significant structural variation, like *Eurylychnus* and *Barypus*, or having a large number of species without a clear synapomorphy. The latter is the case for *Promecoderus*, wich has 41 species assigned to five different terminal units in this analysis.

OUTGROUPS: According to Erwin (1985), the subfamily Broscinae includes the tribes Broscini, Apotomini, and Melaenini. Goulet (1983) had previously proposed a closer relationship between Broscini and Elaphrini, because species of both tribes share the presence of sclerites X and Y (after Ball, 1956) in the internal sac. These structures appear to be plesiomorphic or highly homoplastic as suggested for their presence in nonrelated tribes Melaenini and Paussini. They might be also homologous to the basal stylets of the endophallus of Scaritini (Roig-Juñent, 1998). Larval characters suggest that Elaphrini might be related to Migadopini because they both have two larval claws, and not to the Broscini, which have one (Erwin, 1985). Recently Roig-Juñent (1998), using several tribes of carabid beetles, tested the Erwin and Goulet proposition. The analysis shows that Broscinae is a monophyletic group, and the genera included in the tribe Broscini constitute a monophyletic group, with the tribes Melaenini and Apotomini as its sister groups.

CHARACTERS

The 73 characters used in the analysis were taken from the external morphology (49), aedeagus (13), and female genitalia (11). The distribution of states among the terminal taxa is indicated in the data matrix (table 1). Apomorphic character states are shown on the cladograms (figs. 14, 15) as superscripts. Character states were coded in graded linear series when possible, so that the most divergent states were at opposite extremes. The characters 2, 7, 9, 10, 22, 24, 39, 44, 53, 61, 65, and 66 were treated as nonadditive (unordered) because their pattern of divergence appeared too complex to be arranged in a graded series.

Character polarity was determined by the outgroup comparison method (Watrous and Wheeler, 1980; Maddison et al., 1984).

The data set was analyzed using Farris's phylogenetic package, Hennig86 version 1.5 (Farris, 1988), and applying the heuristic method options. A second analysis was con-

ducted by the successive weighting procedure (Farris, 1969). This second analysis, which is based on the topology of the first analysis, discriminates characters with high value (less homoplasy) versus characters with low value (more homoplasy) to construct the cladograms.

Head

Supraorbital anterior setae (characters 1 and 2): Jeannel (1941) considered two main groups of tribes (families) within Limbata Stylifera, based on the presence of supraorbital setae, anterior and posterior to the eye. According to Jeannel, one of these groups has two supraorbital setae, whereas the other has only the posterior seta. Nevertheless, the anterior and posterior setae are independent, and sometimes the anterior seta is present while the posterior is absent. For this reason I consider these setae as two independent characters.

1. Supraorbital anterior setae: present (0); absent (1).

2. Supraorbital posterior setae: absent (0); one supraorbital puncture bearing one seta (1); two or more punctures, each bearing only one seta (2) (figs. 155, 166, 290); one puncture bearing more than one seta (3) (figs. 175, 189, 200). UNORDERED.

3. Temporal ridge (figs. 1, 2): This suture is like a ridge, more or less distinct, on both sides of the head and extending backward below and behind the eyes (Sloane, 1890). This is the "suture temporale" of Putzeys (1868), and the "sub-ocular ridge" of LeConte and Horn (1883). This structure presents three different states: absent (0); incomplete, when only the posterior portion near the prothorax, is distinct (1) (fig. 2, tr); complete, when this structure is distinct on the entire lateroventral surface of the head (2) (fig. 1, tr).

4. Suborbital ridge: This is a ridge in the ventral region of the preocular area (fig. 3, sbr): absent (0); present (1).

5. Subocular zone (figs. 1, 2, sz): wide (0); narrow (1).

6. Anteocular area: width between supraorbital sulcus and antennal insertion (figs. 1, 2, ae): narrow (0); wide (1).

7. Frontal sulcus: absent (0); broad and straight (1); narrow and curved (2) UNORDERED.

8. Scrobal setae: present (0); absent (1).

9. Number of submentum setae: two (0); four (1); from six to eight (2) UNORDERED.

10. Mentum tooth: absent (0) (figs. 229, 240, 264); developed as a slight convexity (1) (fig. 276); distinct and simple (2) (figs. 18, 26); bifid apex (3) (fig. 34); markedly bifid (4) (fig. 207). UNORDERED.

11. Lateral lobes of mentum: present (0); absent (1).

12. Mentum foveae: absent (0); with two deep and rounded foveae beside the tooth (1).

13. Number of mentum setae: two (0); absent (1).

14. Longitudinal medial carina of the glossal sclerite: I consider such structure true medial carina they clearly extend ventrally from the apical margin (figs. 11, 177, 241). Some creobiine genera have the paramedian parts of glossal sclerite slightly deepset, leaving the central apical part with the appearance of a medial keel (fig. 10). I do not consider the latter a true medial carina. Absent (0) (fig. 10); small (1) (fig. 11); pronounced (2) (fig. 177).

15. Number of glossal sclerite setae: none (0); two (1); four (2).

16. Paraglossa length: long (0) (fig. 177); short (1) (fig. 35).

17. Shape of stipes: outer side not expanded (0); enlarged (1) (fig. 203).

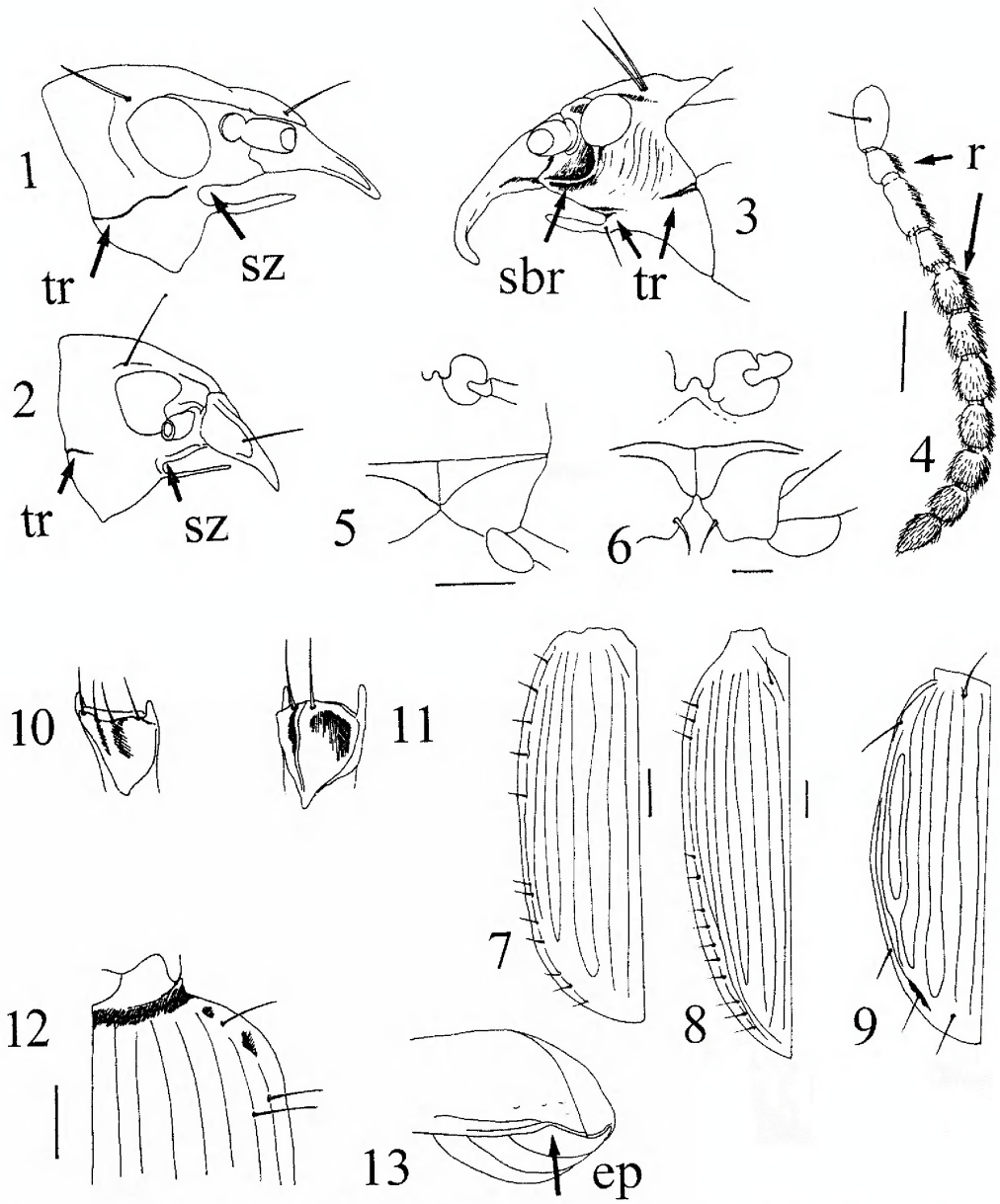
18. Number of basal stipital setae: one (0); two (1); three (2).

19. Setae on second and third segment of maxillary palpi: absent from both segments (0); one seta on each segment (1); two setae on each segment (2).

20. Sides of the gula: smooth (0); with two oblique deep foveae or sulcus (1).

21. Eyes: rounded (0); with an emargination in front of the antennal insertion (1).

22. Antennal pubescence: segment 3 setose on at least its apical half, segments 4–11 setose throughout (0); segment 3 with only an apical ring of setae, segment 4 setose on its apical half or third, 5–11 setose throughout (1); segments 3 and 4 with an apical ring of setae, 5–11 setose throughout



Figs. 1–13. Structural features of broscine adults. Head, right lateral view of (**1**) *Miscodera arctica*; (**2**) *Barypus pulchellus.*(**3**) Head, left lateral view of *Mecodema howitti*; (**4**) antenna of *Barypus pulchellus*. Metasternum ventral aspect of (**5**) *Miscodera arctica*; (**6**) *Barypus speciosus*. Elytron, dorsal aspect of (**7**) *Nothobroscus chilensis*; (**8**) *Oregus aereus*; (**9**) *Cascellius septentrionalis*.Ventrolateral view of glossal sclerite of (**10**) *Creobius eudouxy*; (**11**) *Nothobroscus chilensis*. (**12**) Elytra shoulders of *Metaglymma oblongum*; (**13**) *Apotomus* sp. See appendix 2 for abbreviations.

(2); segments 3–5 with an apical ring of setae (3). UNORDERED.

23. ROW OF POSTEROLATERAL SETAE OF ANTENNAL SEGMENTS 2–5: absent (0); present (1) (fig. 4).

THORAX

24. SHAPE OF PRONOTUM: as in figs. 17, 25 (0), as in fig. 72 (1), as in fig. 228 (2). UNORDERED.

25. PROTHORAX PUNCTUATION: all along the surface (0) (figs. 17, 25); reduced at the base (1) (figs. 81, 93); absent (2).

26. ANTERIOR EDGE OF PROSTERNUM: with a continuous border (0); smooth, without border (1).

27. ANTERIOR COXAL CAVITIES: with two perforations (Jeannel, 1949) or bridged (Bell, 1967) (0); with one perforation or unbridged (1).

28. APICAL PROSTERNAL SETAE: absent (0); present (1).

29. MESEPIMERA (BASE OF THE ELYTRA): shallow (0); with a carina (1).

30. METEPIMERA: not visible or fused (0); visible, not fused (lobulate) (1).

31. METASTERNUM LENGTH: long, more than two times longer than metacoxae (0) (fig.5); short, less than 1.5 times longer than metacoxae (1) (fig. 6).

32. ANTECOXAL SUTURE OF METASTERNUM: visible (0); not visible (1).

ELYTRA

33. PARASCUTELLAR STRIOLE: isolated from the apical portion of stria 1 (figs. 7, 8) (0); joined to the apical portion stria 1 (fig. 9) (1).

34. PARASCUTELLAR SETA (BASAL SETA OF THE SECOND STRIA): present (0); absent (1).

35. INTERVAL 6–7: smooth (0); with an accessory stria (1) (fig. 8); with a double accessory stria, forming circles (2) (fig. 9).

36. WINGS: fully developed (0); small or very small (1).

37. ELYTRA HUMERUS: without groove (0); with groove (1) (fig. 12).

38. ELYTRAL PLICA: present (0) (fig. 13); absent (1).

ABDOMEN

39. ABDOMINAL STERNA: smooth (0); lateral basal sulcus and a shallow fovea on each side (1) (fig. 317); only with lateral fovea (2) (fig. 318); with a complete basal sulcus (3). UNORDERED.

40. SHAPE OF TERGITE 8 OF FEMALE (after Deuve, 1988): nebridian (0); harpalidian (1).

LEGS

41. APEX OF FORETIBIA: not expanded (0); slightly expanded (1); markedly expanded (2) (fig. 225).

42. APEX OF MIDDLE TIBIA: not expanded (0); slightly expanded (1); markedly expanded (2).

43. MESOTIBIAL OBLIQUE COMB (Erwin 1978): present (0); absent (1).

44. FORETARSAL ADHESIVE VESTITURE OF MALE: The only type of adhesive vestiture in Broscini, when present, is the articulo-setae (Stork, 1980). This adhesive vestiture can be distributed on: the first four tarsites (0); the first three tarsites (1); the first two tarsites (2); absent (3). UNORDERED.

45. MIDDLE TARSAL ADHESIVE VESTITURE OF MALE: absent (0); present (1).

46. HIND FEMUR SETAE: in a row (0); not aligned (1).

47. HIND COXAL CAVITY: covered (0); uncovered (1).

48. HIND COXAE: joined at middle (0) (fig. 5); separated at middle (1) (fig. 6).

49. HIND TROCHANTER SETA: absent (0); present (1).

MALE GENITALIA

50. RING OF STERNUM 9: complete and with lateral margins wide (0); complete and with lateral margins narrow (1); incomplete (2).

51. RIGHT PARAMERE: styliform (0); triangular (1).

52. LEFT PARAMERE: setose (0); asetose (1).

53. LEFT PARAMERE (SHAPE): triangular (0) (fig. 36); narrow at apex (1); markedly extended at apex (2) (figs. 278, 286); enlarged (3) (figs. 20, 208, 215). UNORDERED.

54. MEDIAN LOBE, BASAL ORIFICE: completely open (0); partially open (1); closed (2).

55. MEDIAN LOBE, DORSAL SURFACE: completely membranous (0); sclerotized (1).

56. MEDIAN LOBE, BASAL EXPANSIONS: absent (0); present (1).

57. MEDIAN LOBE, BASAL KEEL: absent (0); small (1); complete (2).

58. MEDIAN LOBE, APICAL ORIFICE: open to the right (0); open to the left (1).

59. INTERNAL SAC, SCLERITE X: This sclerite is on the basal portion of the internal sac, and it is a quite complicated structure with several variations. Three features were considered to establish the states: 1—width of sclerite and presence of a central constriction (fig. 41, 69, C); 2—number of points on its

basal region (fig. 196, P); and 3—absence or presence and form of the lateroapical projections (figs. 41, 78, 88, ae). The sclerite X shows the following states: absent (0); thin, without central constriction, with one apical point, and without lateroapical projections (1) (figs. 30–31); broad, with central constriction, with three points and without lateroapical projections (2) (figs. 183–184); like 2, but with two symmetric lateroapical upturned projections (3) (figs. 68–69); like 2, but with asymmetric lateroapical upturned projections (4) (figs. 78–79, 90–91).

60. INTERNAL SAC, SCLERITE Y: absent (0); present (1).

61. INTERNAL SAC, APICAL PLATE: absent (0); composed completely of free spiculae (1) (fig. 57, ap); composed of spiculae free and a central tooth (2) (fig. 127, t); all spiculae fused forming a plate (3) (fig. 141, 150, p). UNORDERED.

62. INTERNAL SAC, TOOTH OF THE APICAL ORIFICE: absent (0); present (1) (figs. 236, 246, 270, th).

FEMALE GENITAL TRACT

63. RAMI OF GONOCOXITE 9: absent (0); short (1); long (2).

64. NEMATIFORM SETAE OF SUBAPICAL SETOSE ORGAN: present (0); absent (1).

65. ACCESSORY GLAND OF BURSA COPULATRIX: absent (0); apical, near the spermatheca (1); medial, far from the spermatheca (2). UNORDERED.

66. LIGULA BASALIS (after Deuve, 1993): absent (0); with ligular apophysis not sclerotized (1); with ligular apophysis sclerotized as an apical plate (2) (figs. 249, 260, lg); a sclerotized ring (3) (fig. 323). UNORDERED.

67. SCLERITE IN THE WALL OF THE BURSA COPULATRIX, ON BASE OF OVIDUCT: absent (0); present (1) (fig. 71, sc).

68. SPERMATHECA AND OVIDUCT: separated (0); joined (1).

69. SPERMATHECAL BASE: thin (0); broad (1).

70. ACCESORY GLAND OF THE SPERMATHECA: absent (0); present (1).

71. BASAL SCLERITE OF ACCESSORY GLAND: absent (0); U shaped (1).

72. VAGINAL APOPHYSIS: absent (0); present (1). Deuve (1993) considered the "vaginal apophysis" a sclerotized fold of the tegument, which is situated between the base of the oviduct and the spermatheca, and joined to urite 9 by muscles, being different from the helminthoid sclerite.

73. HELMINTHOID SCLERITE: absent (0); small (1); broad and short (2) (figs. 50, 60, 102, hs); thin and long (3) (figs. 42, 71, 80, 91–92, hs); broad and long, with the apical region separated from the vaginal apophysis (4) (figs. 174, 187–188, 199, hs).

RESULTS

CLADISTIC ANALYSIS OF BROSCINE GENERA

The analysis of the data matrix (table 1) yielded 60 most parsimonious cladograms with a length of 283, consistency index of 0.39, and a retention index of 0.79. The strict consensus tree (fig. 14) shows that the relationships among the genera are mostly resolved, except for *Eurylychnus* A and B, *Nothobroscus*, the genera of Creobiina with four setae in the glossal sclerite, and *Barypus* subgenera.

The successive weighting procedure yielded 45 cladograms, none of them included in the original 60 trees. The topology of strict consensus tree (fig.15) is congruent with that obtained using equal weights (fig. 14), with the difference that the 45 cladograms show a resolved relationship for *Eurylychnus*, *Nothobroscus*, and the subgenera of *Barypus*. This cladogram (fig. 15) also shows a partially resolved relationship of creobiine genera with four setae in the glossal sclerite. Nevertheless the relationships of *Axonya*, *Broscodes*, and *Rawlinsius* are not resolved.

Results of the cladistic analysis (fig. 15) support the monophyly of the tribe Broscini. Several characters that support Broscini revert or change to other states within the tribe, such as: temporal ridge incomplete (3^1); mentum with a single tooth (10^2); two setae on the stipes (18^1); fourth antennal segment with the apical third pubescent (22^1); elytral plica absent (38^1); male with foretarsomeres 1–2 with adhesive vestiture (44^2); hind trochanter with setae (49^1); apical plate of internal sac present (61^1); rami of gonocoxite 9 long (63^2); ligula basalis absent (66^0); and helminthoid sclerite short and broad (73^2).

Other characters are constant synapomorphic features of Broscini within Broscinae, such as the absence of mesotibial oblique comb (43^1) (present in *Melaenus* and *Apotomus*) and the shape of the tergite 8 (40^1). The primary dichotomy of the cladogram (fig. 15) splits the genera into two major branches. One branch includes three monospecific genera: *Axonya*, *Broscodes,* and *Rawlinsius*, and the second includes all the remaining genera. The second divergence splits Holarctic and Oriental from Austral genera. The Holarctic-Oriental genera are grouped in the subtribe Broscina. The other clade includes Barypina, Creobiina, and the austral genera with sclerites in the internal sac. The third divergence splits the austral genera with sclerite X and Y from Creobiina and Barypina. The fourth main divergence splits the austral groups Creobiina and Barypina.

The Bremer supports show that all clades are well supported (fig. 16). The less supported clades are the basal node of Broscini (with 9) and the basal clade (*Rawlinsius*, *Axonya*, and *Broscodes*) with 10. Strongly supported clades are the austral Broscini with sclerite X (with 28) and *Microbarypus* and *Barypus* (with 28).

Character Analysis

Table 2 shows the weighted values of several characters that support the classification of Broscini proposed here. Following are comments about some of them and about other characters previously used (Jeannel, 1941; Ball, 1956; Britton, 1949).

Male Aedeagus

1. Internal sac, apical plate (character 61): This structure is absent from the outgroups, and its presence, formed by free spiculae, is a plesiomorphic condition within Broscini. Three apomorphic states are present: fusion of its central spiculae in a central tooth (fig. 185); or all the spiculae forming a plate (fig. 150); or loss of this structure from Barypina-Creobiina. This character shows a high value (table 2).

2. Internal sac, sclerite X (character 59): This is the most diverse structure in the internal sac, showing a complex evolution in shape and apical projections. The cladogram shows that a thin sclerite without apical and basal projections (figs. 30–32) is the plesiomorphic condition of this structure in Broscini, that remains only in the basal genera *Axonya*, *Broscodes*, and *Rawlinsius*. From this condition, sclerite X evolves to a broad structure, with constriction and basal expansions (figs. 171–172). From this latter condition, it evolves to a structure with upturned basal projections in Broscina (figs. 40–41), remaining without them in Nothobroscina. The sclerite X is lost in the Barypina-Creobiina node. This character has a large value in the classification (table 2).

3. Ring of sternum 9 (character 50): The plesiomorphic condition for this character is with apodemes of the sternum 9 narrow and forming a ring. Two apomorphic states evolved independently from this condition: first the apodemes are wide, and form a ring in Nothobroscina; and second the apodemes are narrow but not fused, forming a ring in two groups of Creobiina where this latter state has evolved independently. This character has a medium value in the classification (table 2).

4. Median lobe, basal orifice (character 54): Jeannel (1941) used this character to subdivide the tribe, considering three different states: completely closed (Barypina), partially closed (Broscina), and completely open (Creobiina). Ball (1956) discussed the value of this character, and pointed out that Jeannel's system includes *Axonya* (a genus with the basal orifice completely open, fig. 24) in Broscina (table 3), and the genera *Miscodera* and *Broscosoma* (two genera with the basal orifice completely closed) in Creobiina.

The cladogram shows that the basal orifice evolves from a plesiomorphic condition (completely open) in Apotomini, Melaenini, and Axonyina to a partially closed condition in the Broscina-Nothobroscina-Barypina-Creobiina node. It remains in this condition in the Broscina, evolving to a completely closed condition in Barypina-Nothobroscina-Creobiina, and reverts to the plesiotypic condition in Creobiina. The closure of basal orifice has a lower value for the classification (table 2).

5. Internal sac, sclerite Y (character 60): Its presence is a plesiomorphic condition and its loss in Barypina-Creobiina is one of

TABLE 1
Data Matrix of Broscini Genera
Plesiomorphic states = 0, apomorphic states = 1–5, missing data = ?

	Characters					
	11111111112222	222222333	33333334	444444444	5555555555666	66666667777
Genera	12345678901234567890123	456789012	34567890	123456789	0123456789012	34567890123
Melaenini	00000000030000100020020	000100000	11100030	000300010	1003000001100	00110000011
Apotomini	11001000001000110000000	100000000	10100000	000300000	1100001000000	00110000000
Broscodes	11101000220000110200010	001100000	10100101	001110001	1003001001110	????????????
Axonya	11101000120000110200010	001100000	10100001	001110001	1003001001110	????????????
Rawlinsius	10??100102000011020010	00110002?	0110010?	001300001	?003001001110	10200000012
Zacotus	1110001?220000110101020	010100000	00010101	001110011	1000110003110	20101000113
Eobroscus	11200010220000110?01010	010100000	00010101	001210001	?000110003110	????????????
Miscodera	11201010220100110100020	110100000	10000101	001110000	1000110004110	20201000013
Broscosoma	11100010220000110100010	110100000	10010101	001110001	10?0110004110	20101000012
Broscodera	11201010220100110?00010	110100000	10000101	001110001	1001110004110	10101000013
Broscus	112000?0??000011010020	010100000	10000101	001101000	1000110003110	20101000113
Chaetobroscus	12200000220000110100010	011100000	11010101	001200001	1000110003110	11101000112
Craspedonotus	11200000020000110100010	001100000	00000101	001301000	1000110003110	20101000112
Nothobroscus	11100020030101100100020	020100110	11010101	001300011	0001210002120	20201000013
Diglymma	11200010?30101100100010	020100110	00010101	001200011	0011210002110	20201000012
Eurylychnus A	11100020230101100100010	020100110	11110101	001201011	0010210002120	20201000012
Eurylychnus B	11100020030101100100020	021100110	01010101	001301011	0010210002120	20201000012
Chylnus	1?1000?1030101100100020	220100110	11010101	001301011	0010210002130	10101000012
Percolestus	11100001030101100100020	220100110	11010101	001301011	0011210002130	10101000013
Oregus	1210000?130002100200010	221100110	00110101	001301011	0011210102120	21101000012
Percosoma	12111001240002101200020	021100110	11010101	001301011	0001210102120	21100000014
Metaglymma	13110001240002101100030	021100110	11011101	221301011	0001210002120	21100000014
Brullea	13110001240002001100030	0?1100110	11011101	221301011	?001210?021?0	21100000014
Mecodema	13110001240002101100020	0?1100110	11010101	111301011	0001210002120	21100000014

TABLE 1
Continued

Genera	Characters					
	11111111112222	222222333	33333334	444444444	5555555555666	66666667777
	12345678901234567890123	456789012	34567890	123456789	0123456789012	34567890123
Arathymus	11100100040002100200121	221110110	01010131	001301011	1013210210000	10000110000
Barypus	11100110140002100200121	221110110	01010131	001201011	1013210210000	21000110000
Cardiophthalmus	11100100040002100200111	221110110	01010131	001201011	1013210210000	21000110000
Microbarypus	11201100230001100210110	221110110	01010101	001210011	1001210110000	20000100000
Creobius	12100000020000210100000	220100100	10210111	001010011	1012001000000	11110010000
Cascellius	11200000010000210100000	220100100	10210111	001010011	1012001000000	01210110000
Nothocascellius	11100000020000210100000	220100110	10010111	001?00011	10?2001000000	11000000000
Promecoderus A	11200000110000210100000	220100100	10210101	001010011	2012001000000	11000000000
Promecoderus B	11200000120000210100000	220100100	10210121	001110011	2012001000000	11210110000
Promecoderus C	11200000120000210100010	220100100	10210121	001110011	1012001000000	11230110000
Promecoderus D	11200000120000210100010	220100100	10210121	001010011	1012001000000	11210110000
Promecoderus E	11200000120000210100010	220100100	10210111	001010011	2012001000000	11230110000
Anheterus	11200000120000210100010	220100100	10210121	001300011	1012001000000	11210110000
Acallistus	11200000110000210100010	220100100	10210101	001100011	1012001000000	11000000000
Bountya	11?0000?220000210100010	2201001?0	?0?10101	001300011	?012001000000	?1000000000
Cerotalis	11200000000002111100010	220101111	10110101	001010011	1002001010001	01010001000
Adotela	11200000?00002111110010	220101111	10010101	111100111	1012001010001	01020001000
Gnathoxys	11200?0000012111210020	2201?1111	10010101	221300111	1012001010000	01020001000
Brithystemum	11200000000012111210020	220101111	10010101	001300111	1012001010001	01020001000

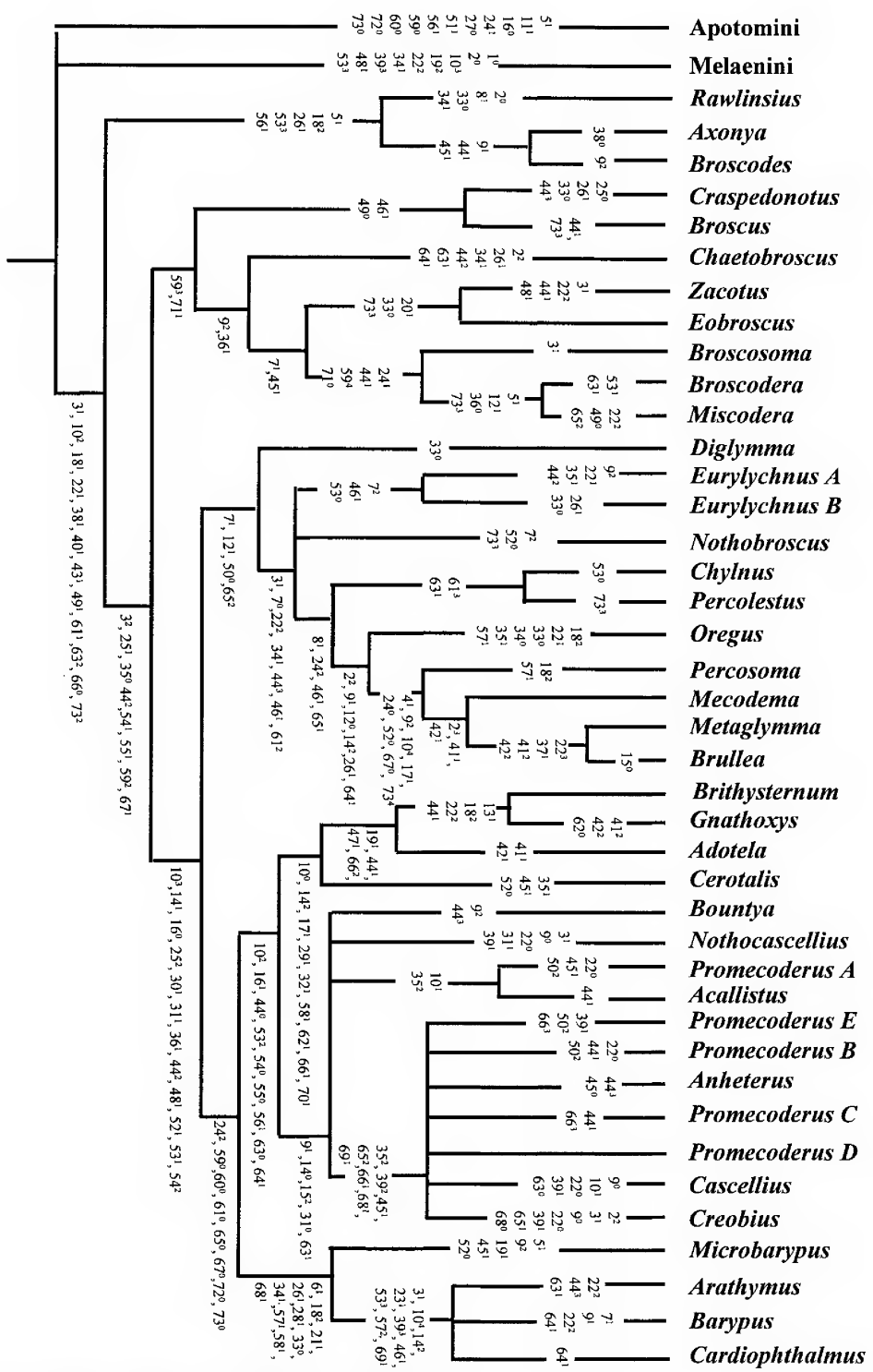


Fig. 14. Strict consensus tree from the 240 cladograms obtained by equal weighted parsimony.

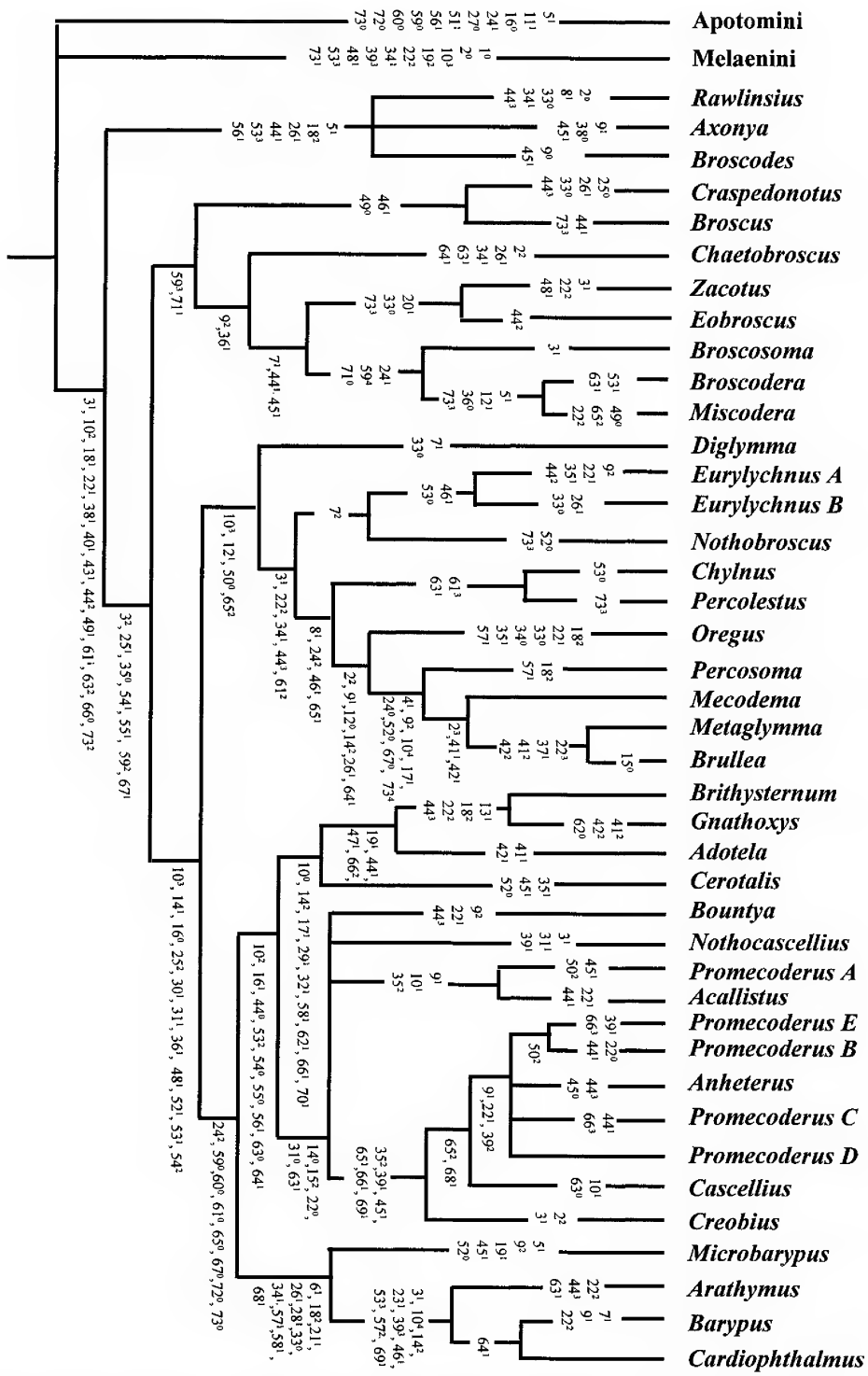


Fig. 15. Strict consensus tree from the 15 cladograms obtained by successive weighting procedure.

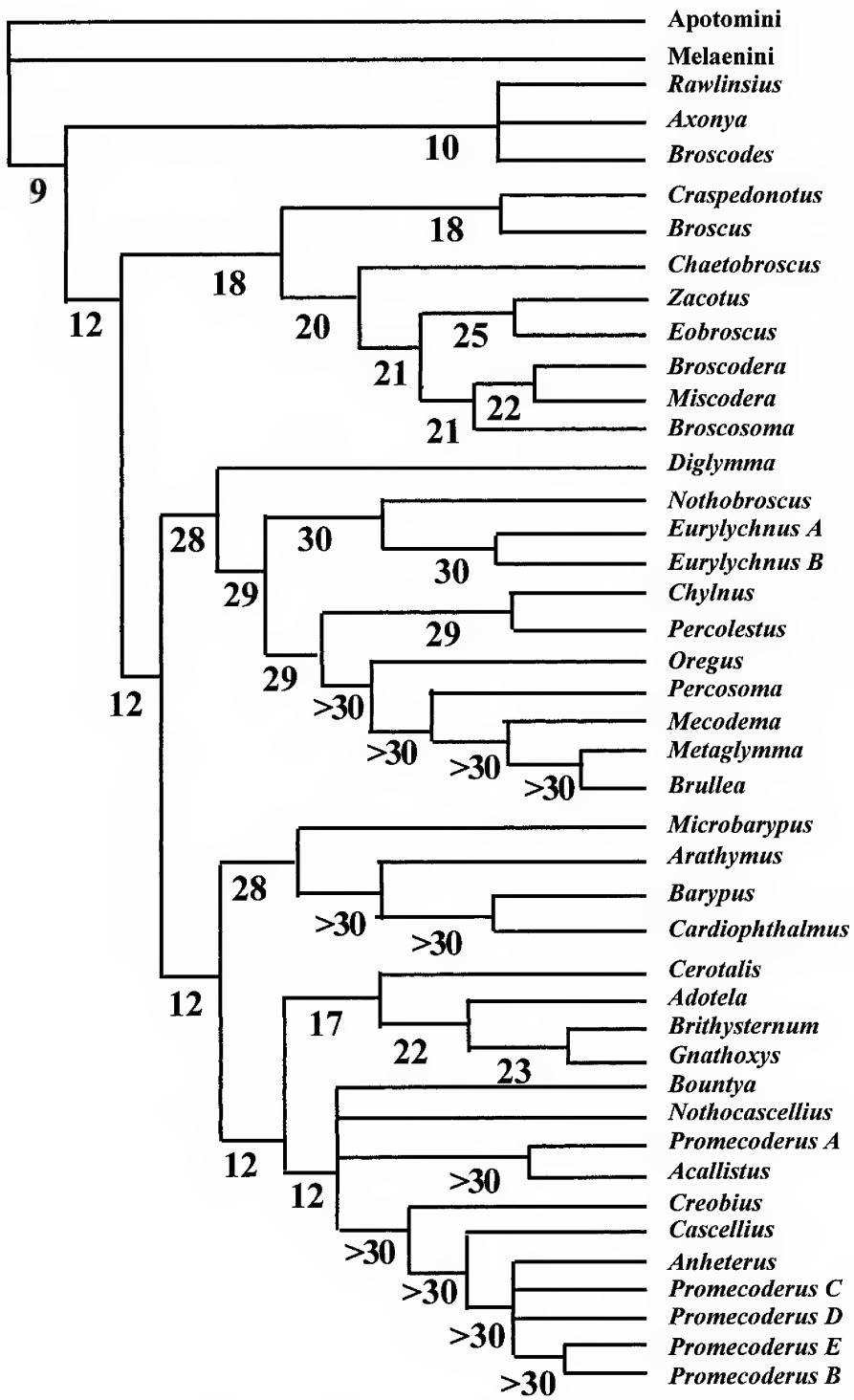


Fig. 16. Bremer support of Broscini clades.

TABLE 2
Character Weight After Successive Weighting Procedure

	Character number		
Weight	External morphology	Aedeagus	Female gen. tract
10	1, 4, 6, 11, 13, 15, 20, 21, 23, 27, 28, 29, 30, 32, 37, 40, 43, 47	51	70
7	—	61	—
6	25	59	—
5	—	50	—
4	8, 17, 31	54, 55, 58, 60	68, 69, 72
3	7, 10, 14, 24, 39	53, 57	66, 71, 73
2	2, 12, 16, 18, 19, 35, 36, 38, 41, 42, 48	56, 62	64, 65, 67
1	3, 5, 9, 26, 34, 46, 49	52	63
0	22, 33, 44, 45	—	—

the synapomorphic states that joins these two subtribes. Although this structure is always present with sclerite X, after the successive weighting procedure, it has a lower value than sclerite X, and has the same value as the dorsal surface of median lobe, apical orifice, and basal orifice of median lobe (table 2).

6. MEDIAN LOBE, DORSAL SURFACE (character 55): This character appears to relate to the presence of basal expansions (character 56) because all genera that have the dorsal surface completely membranous have basal expansions except *Melaenus*, which has the dorsal surface membranous, but lacks the basal expansions. The dorsal surface evolves from a surface completely membranous in Apotomini and Axonyina to a sclerotized one in the node of the remaining Broscini. In Creobiina, it reverts to the plesiomorphic condition.

7. MEDIAN LOBE, APICAL ORIFICE (character 58): This structure is open to the right in all broscines, except in Barypina and Creobiina. The analysis shows a low value for this structure because it is present also in Apotomini, but within Broscini it is an important character.

8. MEDIAN LOBE, BASAL KEEL (character 57): Ball (1956) proposed this character as an autapomorphic state of Barypina. Nevertheless, it is present at variable degrees in genera of Nothobroscina, as *Oregus* and *Percosoma*, and shows a low value for the classification of Broscini.

9. MEDIAN LOBE, BASAL EXPANSIONS (character 56): This structure is present in Apotomini and Axonyina, and it is lost in the node of the remaining Broscini. In Creobiina, it reverts to the plesiomorphic condition. This character has one of the lowest values (table 2).

FEMALE GENITAL TRACT

Except for the accessory gland of spermatheca (character 70) that defines one group of Creobiina, the remaining characters of the female genital tract have low values.

EXTERNAL MORPHOLOGY

In general terms, the external morphological characters with high values define small groups of genera or are autapomorphic. Nevertheless, some characters constitute synapomorphies of Broscini, like shape of tergite 8 (character 40) and mesotibial oblique comb (character 43); others support the node Nothobroscina-Barypina-Creobiina: the shape of metepimera (metepimera lobate, character 30); the node Nothobroscina-Barypina-Creobiina-Broscina (elytral plica absent, character 38); or some group like Barypina (shape of anterolateral ocular area, character 6, eyes emarginate, character 21, and apical prosternal setae, character 28).

Some characters of the external morphology discussed by Ball (1956) and Townsend (1971) have a different value for the systematics of Broscini:

1. LONGITUDINAL MEDIAL CARINA OF THE GLOSSAL SCLERITE (character 21): The subtribe Creobiina was characterized by the keeled glossal sclerite (Townsend, 1971), but only four genera have this structure; the genera with glossal sclerite quadrisetose, like *Promecoderus* and related genera, have the paramedian parts of the glossal sclerite lightly deep-set, leaving the central apical part with the appearance of a medial keel. Ball (1956) characterized the Broscina of New Zealand as having a markedly keeled glossal sclerite, but this feature is also present in Barypina and the Creobiina genera *Cerotalis*, *Gnathoxys*, *Adotela*, and *Brithysternum*.

2. GLOSSAL SETAE (character 15): The number of glossal sclerite setae is a constant and a good character. Four glossal sclerite setae are synapomorphic for a clade of Creobiina.

3. THE PRESENCE OR ABSENCE OF SCROBAL IN THE MANDIBULAR SCROBE (character 8): Ball (1956) gave this character a low value because of its variability, even within some species. My analysis also shows that this character has a low value (table 2). Nevertheless, the complete absence in all the specimens examined of genera like *Mecodema* or *Metaglymma* constitutes a synapomorphy within Broscini.

4. PARASCUTELLAR STRIOLE (character 33): This is another character given a low value by Ball (1956). It shows a value of zero in my analysis.

5. ELYTRA UMBILICAL SERIES: Ball (1956) also noted the number of punctures in the umbilical series: "the umbilical series vary to such an extent through the Broscini that their taxonomic value must be slight"; this character has not been considered because it presents overlapping ranges between species.

6. ADHESIVE VESTITURE OF MALE TARSOMERES: Morita (1990) stated that the presence or absence of adhesive vestiture on the ventral surface of tarsi and the number of setae on sternum 7 (anal sternum) in the male are regarded as important characters at the subgeneric or generic level. The first character (considered here as two different characters, 44 and 45) is of low value (zero in this analysis), since species of the same genus (even subgenera such as *Cardiophthalmus* or *Barypus*) have or lack this structure, and the cladogram (fig. 16) shows that this character has several parallel gains and losses. The second character mentioned by Morita (1990) was not considered in this analysis because the number of umbilical setae was not included.

SYSTEMATIC ACCOUNTS

BROSCINI HOPE, 1838

Broschidae Hope, 1838 (misspelling): 80.
Broscides: Putzeys, 1868: 305; 1873: 307.
Cnemacanthides Lacordaire, 1854: 237. Castelnau, 1868: 159.
Zacotini Horn, 1881–1882: 169.
Broscini Sloane, 1920: 124. 1923: 244. Csiki, 1928: 8. Andrewes, 1935: 32. Jeannel, 1941: 286. 1949: 1044. Emdem, 1942: 30. Blackwelder, 1944: 28. Britton, 1949: 533. Ball, 1956: 40. Kryzhanovskij, 1976: 61. Reichardt, 1977: 395. Erwin, 1979: 588. 1984: 374. Erwin and Sims, 1984: 359.

TYPE GENUS: *Broscus* Panzer, 1813.

DIAGNOSIS: Antennomeres 1–2 glabrous, 3 glabrous or only with apical ring of setae; from one to many supraorbital setae; mandibles with or without scrobal seta; forecoxal cavities uniperforate; middle coxal cavities closed by sterna (conjunct); foretarsomeres of male with or without adhesive vestiture, if present constituted by articulo-setae; female abdomen harpalidian, female tergite 8 simple; defensive gland simple, opened between the 8th and 9th segment; aedeagal parameres long, right setiferous, left setiferous or not; gonopodites dimerous; Larvae: with one tarsal claw.

COMPARATIVE NOTES: The two related tribes are Apotomini and Melaenini. Broscini differ from Apotomini in having prothorax with lateral margin; head, thorax, and abdomen lacking pubescence all along surface; and foretibiae without the apical region notched. Melaenini differs from Broscini in having anterior supraorbital setae.

TAXONOMIC HISTORY: Broscini was defined by Hope (1838) as including the genera *Broscus*, *Miscodera*, and *Stonis* Clarville, and sharing its history with Cnemalobini (=

TABLE 3
Classifications Proposed by Jeannel (1941) and Ball (1956)

Barypina	Creobiina	Broscina
Jeannel Classification (1941)		
Barypus	*Creobius*	*Axonya*
Brullea	*Broscodes*	*Broscus*
Mecodema	*Broscosoma*	*Chaetobroscus*
"et nombreux autres"	*Miscodera*	*Craspedonotus*
	Promecoderus	
Ball Classification (1956)		
Barypus	*Cascellius*	*Axonya*
	Cerotalis	*Broscosoma*
	Creobius	*Broscus*
	Gnathoxys	*Brullea*
	Parroa	*Chaetobroscus*
	Promecoderus	*Craspedonotus*
		Diglymma
		Eurylychnus
		Mecodema
		Metaglymma
		Miscodera
		Oregus
		Percosoma
		Zacotus

Cnemacanthini) (Roig-Juñent, 1993). Lacordaire (1854) put 11 genera (including the genus *Cnemalobus* Guérin-Ménéville, 1838) under the name Cnemacanthides. Putzeys (1868) changed the name Cnemacanthides for Broscides, but without excluding the genus *Cnemalobus*. Jeannel (1941) excluded the genus *Cnemalobus* and suggested that this genus is related to Perigonini, now included in the subfamily Harpalinae (Roig-Juñent, 1993).

The higher classification of Broscini has been rather fluid in recent years, because the tribal name Broscini has been used more or less synonymously with the subfamily name Broscinae (Britton, 1949, 1970; Darlington, 1965). Jeannel (1941) elevated the tribes to family rank, dividing the Broscidae into three subfamilies (now subtribes): Broscina, Creobiina, and Barypina (table 3). Both the change of taxonomic category and the classification have been critically examined by Britton (1949) and Ball (1956). Ball (1956) also classified the tribe into three subtribes, but with a different arrangement of genera (1941) (table 3).

The results of the cladistic analysis support a different view of the systematics of Broscini (table 4) because the subtribes proposed by previous authors do not constitute natural groups, except Creobiina sensu Ball (1956). The genera are grouped into five basal clades that are related to one another to various degreess (figs. 14–15). For example, the clade *Barypus-Microbarypus* and Creobiina are more closely related to one another than either is to other clades. Also, four of the clades are more closely related to one another than any of them are to the basal clade constituted by *Axonya*, *Broscodes*, and *Rawlinsius*. Besides, the different relationships within these five clades I will consider all of these groups placed at the same taxonomic level. These five monophyletic groups represent, with small modifications, the subtribes or natural groups proposed by Ball, and the decision of considering them with the same rank is to maintain the stability of the Broscini systematics.

Key to subtribes of Broscini

1. Mentum tooth bifid; basal orifice of median lobe completely closed dorsally 5
- Mentum tooth simple or absent; basal orifice of median lobe completely or partially open dorsally 2

2(1). Glossal sclerite with four setae; if two setae present, then mentum tooth absent; sclerites X and Y absent, spermatheca without basal sclerite ..... CREOBIINA Jeannel, 1941
- Glossal sclerite with two setae, mentum tooth present; sclerites X and Y near the base of the internal sac; spermatheca with a sclerite in vaginal apophysis 3

3(2). Without clypeal, supraorbital, lateral pronotal, and lateral umbilical setae ..... AXONYINA new subtribe (part)
- With clypeal, supraorbital, lateral pronotal, and lateral umbilical setae 4

4(3). Eustipes with three basal setae; metepimera fused with metepisterna, not distinct; pronotum with one medial seta; dorsal surface of median lobe not sclerotized; sclerite X thin and without lateral upturned projections ..... AXONYINA new subtribe (part)
- Eustipes with two basal setae; metepimera not fused with metepisterna, distinct; pronotum with one, two, or more setae; dorsal surface of median lobe partially or not sclerotized; sclerite X broad, with lat-

TABLE 4
Classification Proposed in this Paper

Barypina	Creobiina	Broscina	Axonyina	Nothobroscina
Barypus	*Acallistus*	*Broscodera*	*Axonya*	*Brullea*
Microbarypus	*Adotela*	*Broscosoma*	*Broscodes*	*Chylnus*
	Anheterus	*Broscus*	*Rawlinsius*	*Diglymma*
	Bountya	*Chaetobroscus*		*Eurylychnus*
	Brithysternum	*Craspedonotus*		*Mecodema*
	Cascellius	*Eobroscus*		*Metaglymma*
	Cerotalis	*Miscodera*		*Nothobroscus*
	Creobius	*Sinobrosculus*		*Oregus*
	Gnathoxys	*Zacotus*		*Percolestus*
	Nothocascellius			*Percosoma*

Note: Genus *Ebertius* was not included in the study.

eral upturned projections . . . . . BROSCINA Hope, 1838

5(1). Eyes emarginate; prosternum with setae; sclerites X, Y, and apical plate absent; accessory gland of female tract and spermathecal sclerite absent . . . . . BARYPINA Jeannel, 1941

- Eyes entire; prosternum without setae; sclerite X broad and elongate, sclerite Y and apical plate present; accessory gland of female tract and spermathecal sclerite present . . . . . NOTHOBROSCINA new subtribe

AXONYINA, NEW SUBTRIBE

TYPE GENUS: *Axonya* Andrewes, 1923.

DIAGNOSIS: Mentum tooth simple, glossal sclerite with two setae, basal orifice of median lobe dorsally open, right and left parameres setiferous, sclerite X of internal sac thin, without upturned projections.

INCLUDED TAXA: This new subtribe is proposed for the first clade of Broscini that includes three genera: *Axonya*, *Broscodes*, and *Rawlinsius*. In contrast with to relatively closely related groups of Broscina genera, the members of Axonyina are definitely more remote, and cannot be placed in the subtribe Broscina. No character is exclusive from this subtribe and the characters that define Axonyina are: subocular zone narrow (5^1), basal stipes with three setae (18^2), anterior border of prosternum with edge (26^1), male with foretarsomeres 1–3 with adhesive vestiture (44^1), left paramere enlarged (53^3), and median lobe with basal expansions (56^1). On the basis of the median lobe and sclerites of internal sac, Axonyina appears to be the most primitive member of Broscini.

The three genera of Axonyina are monospecific with restricted distribution and occur in different regions. *Axonya* is Oriental, *Broscodes* is Palaearctic, and *Rawlinsius* occurs in the northern part of Neotropical region.

KEY TO GENERA OF AXONYINA

1. Without clypeal, supraorbital, lateral pronotal, and lateral umbilical setae; submentum with two setae; fore and middle tarsomeres of male without adhesive vestiture . . . . . *Rawlinsius*

- With clypeal, supraorbital, lateral pronotal, and lateral umbilical setae; submentum with more than two setae; male with foretarsomeres 1–3 and middle tarsomeres 1–2 with adhesive vestiture of articulosetae ventrally 2

2(1). Six setae on submentum; elytral plica absent . . . . . *Broscodes*

- Four setae on submentum; elytral plica present . . . . . *Axonya*

Axonya Andrewes, 1923

Figures 17–24

Axonya Andrewes, 1923: 69. Csiki, 1928: 11. Andrewes, 1935: 40. Ball, 1956: 44.

TYPE SPECIES (by monotypy): *Axonya championi* Andrewes, 1923.

DIAGNOSIS: *Axonya* differs from other Axonyina in having four setae on submentum and from all broscine genera in having elytral plica.

DESCRIPTION: External morphology (figs. 17, 18): Head with one supraorbital seta over each eye; temporal ridge distinct at the apical region; antenna with antennomeres 1 and 2 glabrous, 3 with apical ring of setae, 4 setose on apical half, 5–11 setose throughout. Mandibles each with scrobal setae. Maxilla with eustipes with three basal setae. Labium with submentum quadrisetose; tooth of mentum simple; prementum with glossal sclerite bisetose apically, ventral surface without longitudinal carina. Pronotum cordate, moderately constricted apically, with one seta each side. Elytron with parascutellar striole joined to the apical portion of stria 1; parascutellar setae present, on basal portion of second stria; lateral umbilical series with three setae. Foreleg with trochanter bisetose; male with foretarsomeres 1–3 and middle tarsomeres 1–2 with adhesive vestiture of articulo-setae ventrally.

Male genitalia (figs. 19–24): Sternum 9 with sclerotized complete ring with lateral margins narrow (fig. 19). Median lobe with dorsal surface unsclerotized and basal orifice open dorsally (fig. 23). Internal sac with sclerite X thin, without lateral expansions and constriction (fig. 24); apical plate without tooth, with spiculae only. Left and right parameres setiferous apically, along inner margins (figs. 20–21).

LARVAE: The larva of *A. championi* was described by Gardner (1931).

HABITAT: Adults of this species live on river banks, in wet places, running freely on water (Andrewes, 1923).

GEOGRAPHICAL DISTRIBUTION: The single species of *Axonya* is Oriental, occurring in India on the southern slopes of the Himalaya.

MATERIAL EXAMINED: *Axonya championi* (MCZ).

Broscodes Bolívar y Pieltain, 1914

Figures 25–32

Broscodes Bolívar y Pieltain, 1914: 456. Csiki, 1928: 11.

TYPE SPECIES (by monotypy): *Broscodes karunamicus* Bolívar y Pieltain, 1914.

DIAGNOSIS: *Broscodes* is distinguished from other Axonyina in having six setae on submentum.

DESCRIPTION: External morphology (figs. 25–26): Head with one supraorbital seta over each eye; temporal ridge distinct at the apical region; antenna with antennomeres 1 and 2 glabrous, 3 with apical ring of setae, 4 setose on apical half, 5–11 setose throughout. Mandibles each with scrobal setae. Maxilla with eustipes with three setae laterally. Labium with submentum with six setae; tooth of mentum simple; prementum with glossal sclerite bisetose apically, ventral surface without longitudinal carina. Pronotum constricted apically, with one seta each side. Elytron with striae punctuate; parascutellar striole joined to the apical portion of stria 1; parascutellar setae present, on basal portion of second stria; lateral umbilical series with four setae. Foreleg with trochanter bisetose; male with foretarsomeres 1–3 and middle tarsomeres 1–2 of male with adhesive vestiture of articulosetae ventrally.

Male genitalia (figs. 27–32): Sternum 9 with sclerotized ring complete with lateral margins narrow. Median lobe with dorsal surface only sclerotized on the basal third (figs. 27–28) and basal orifice open dorsally (fig. 29). Internal sac with sclerite X thin, without lateral expansions and constriction (figs. 30–32); apical plate without tooth, with spiculae only. Left and right paramere setiferous apically, along inner margins.

GEOGRAPHICAL DISTRIBUTION: The single species of *Broscodes* is Palaearctic, occurring in Turkey.

MATERIAL EXAMINED: Paralectotype male and lectotype male (PRESENT DESIGNATION) of *Broscodes karunamicus* (MNCN).

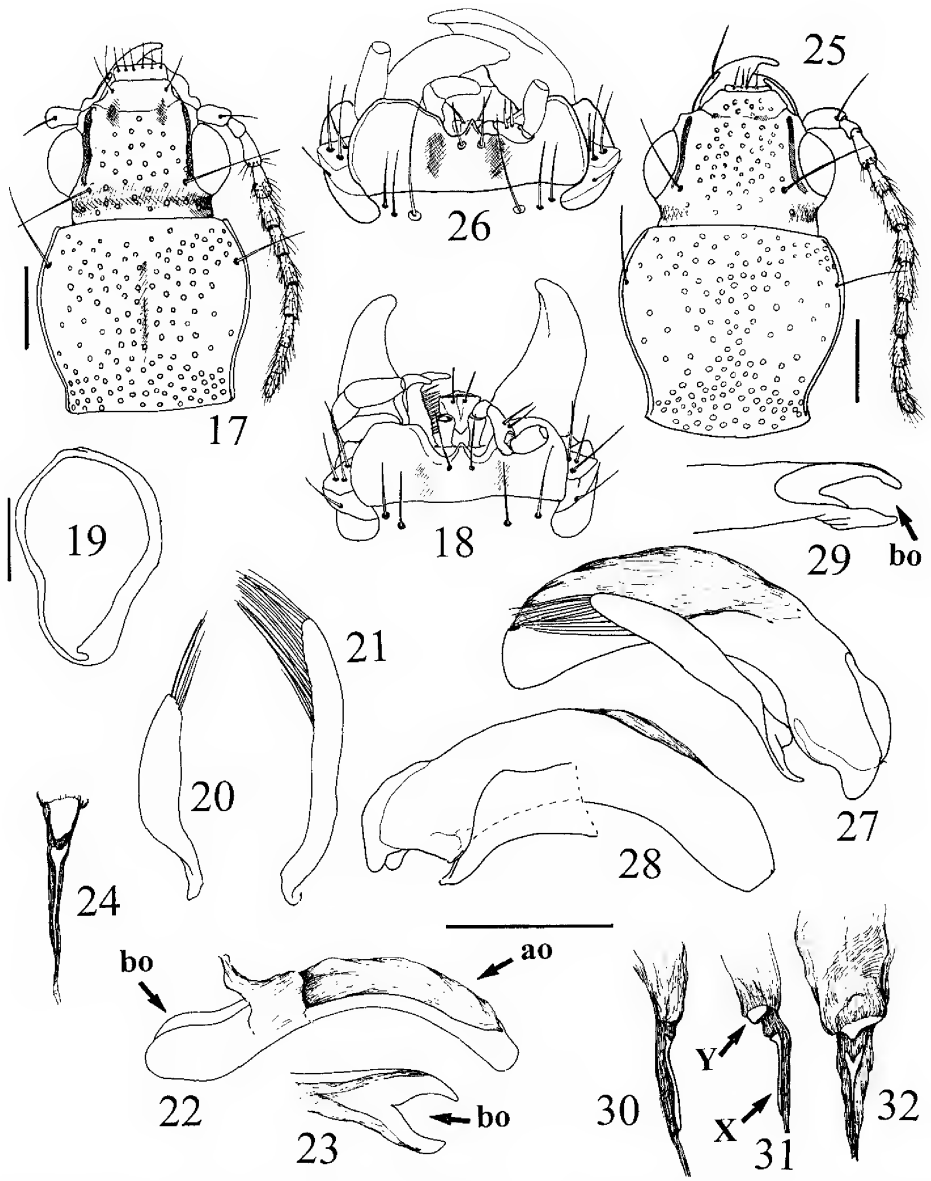
Rawlinsius Davidson and Ball, 1998

Rawlinsius Davidson and Ball, 1998: 361.

TYPE SPECIES (by original designation): *Rawlinsius papillatus* Davidson and Ball, 1998.

DIAGNOSIS: *Rawlinsius* is distinguished from all broscine genera because it lacks the dorsal standard fixed setae: clypeal, supraorbital, antennal scape, lateral pronotal, parascutellar, and lateral umbilical of the elytra.

DESCRIPTION (from Davidson and Ball, 1998): External morphology: Head without supraorbital seta. antenna with antennomeres 1–4 glabrous, with apical fixed setae on 4, 5–10 setose throughout. Mandibles without



Figs. 17–32. *Axonya* and *Broscodes*. (**17–24**) *Axonya championi*: (**17**) head and prothorax; (**18**) mouthparts, ventral view; (**19**) sternum 9; (**20**) left paramere; (**21**) right paramere; (**22**) median lobe; (**23**) base of median lobe, dorsal view; (**24**) sclerite X, dorsal view. (**25–32**) *Broscodes karunamicus*: (**25**) head and prothorax; (**26**) mouthparts, ventral view; (**27**) median lobe with right paramere; (**28**) median lobe, (**29**) base of median lobe, dorsal view; (**30**), sclerite X, lateral view; (**31**) lateral view; (**32**) dorsal view. See appendix 2 for abbreviations.

scrobal setae. Maxilla with eustipes with three setae laterally. Labium with submentum bisetose; tooth of mentum simple; prementum with glossal sclerite bisetose apically, ventral surface without longitudinal carina. Pronotum moderately constricted apically, without lateral seta. Elytron with parascutellar evident; parascutellar setae absent; lateral umbilical series without setae. Fore and middle tarsomeres of male without adhesive vestiture.

Male genitalia: Median lobe with dorsal

surface unsclerotized and basal orifice open dorsally. Internal sac with sclerite X thin, without lateral expansions and constriction; apical plate without tooth, with spiculae only. Left and right parameres setiferous apically, along inner margins.

Female genital tract: Ramus present. Nematiform setae of subapical setose organ present. Spermatheca with helminthoid sclerite broad and short; accessory gland near the spermatheca.

LARVAE: The larval characters of *R. papillatus* are discussed briefly by Davidson and Ball (1998).

HABITAT: Adults of this species live in the overflow of small stream. Davidson and Ball (1998) provided a complete description of habitat and behavior.

GEOGRAPHICAL DISTRIBUTION: The single species of *Rawlinsius* is Neotropical, occurring in Sierra Madre, Mexico.

BROSCINA HOPE, 1838, new concept

TYPE GENUS: *Broscus* Panzer, 1813.

DIAGNOSIS: Mentum tooth simple, glossal sclerite with two setae; basal orifice of median lobe partially closed dorsally; right and left parameres setiferous; sclerite X broad, with upturned apical projections; spermatheca with basal sclerite.

INCLUDED TAXA: This subtribe was characterized by Jeannel (1941) for the genera *Broscus, Chaetobroscus*, *Craspedonotus*, and *Axonya* (table 3). Ball (1956) added the austral genera that have sclerites X and Y (table 3), recognizing three monophyletic groups within the subtribe. The cladistic analysis (fig. 15) presented herein shows that each of these three groups is monophyletic, and each is considered as a different subtribe: Broscina, Axonyina, and Nothobroscina. The subtribe Broscina is the second clade (figs. 14–16) and contains the Holarctic genera that have sclerite X with upturned projections. This new concept coincides with Ball's (1956) concept in including the genera *Miscodera* and *Broscodera*, but differs from it (table 3) in excluding all the austral genera, as well as *Axonya* and *Broscodes* (table 4). Figure 16 shows that Broscina genera share two exclusive derived features: upturned apical projections on the sclerite X (59[3]) and accessory gland of bursa copulatrix with U-shaped basal sclerite (71[1]). Within Broscina there are two main clades, one formed by *Craspedonotus* and *Broscus*, and the other by the remaining genera.

The subtribe Broscina includes nine genera (table 4) and 52 species. Four of these genera are monospecific. It was not possible to study the genus *Tosawabroscus*, because the reference to *Tosawabroscus amabilis* Uéno 1953, cited by Morita (1990) as nomen nudum, was unavailable.

Most species of Broscina are confined to the Holarctic region and inhabit alpine or grassland habitats. However, the genera *Broscodera* and *Zacotus* (both monospecific) occur in coastal forest at low altitude.

KEY TO GENERA OF BROSCINA

1. Labial mentum bisetose 2
- Labial mentum quadrisetose . . . . . *Sinobrosculus*

2(1). Head with one supraorbital seta over each eye; pronotum with one or two lateral setae on each side 3
- Head with three or four supraorbital setae over each eye; pronotum with seven or eight lateral setae on each side . . . . . *Chaetobroscus*

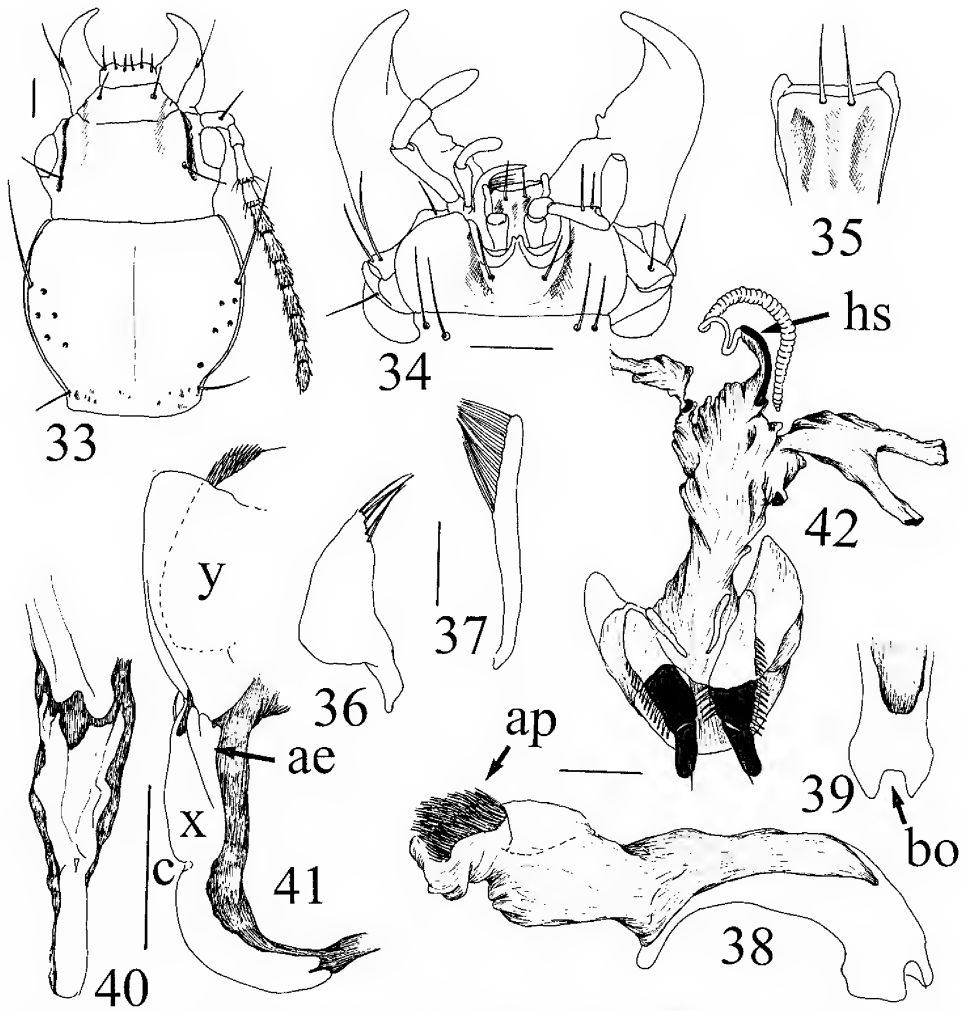
3(2). Head with ventral surface with two deep transverse grooves or oblique foveae on each side of gula 4
- Ventral surface of head without such grooves or foveae 5

4(3). Submentum with six setae, a deep transverse sulcus on neck constriction; median lobe ventrally with "wings" . . . . . *Eobroscus*
- Submentum with 8 to 10 setae; a shallow transverse sulcus on the neck constriction; median lobe without "wings" . . . . . *Zacotus*

5(3). Elytron with parascutellar setiferous puncture at base of stria 2 6
- Elytron without parascutellar setiferous puncture . . . . . *Broscodera*

6(5). Labial mentum with two paramedian rounded foveae; pronotum with one lateral seta near middle . . . . . *Miscodera*
- Labial mentum with ventral surface almost plane, not deeply impressed on each side of tooth; pronotum with two lateral setae on each side 7

7(6). Submentum with a single seta on each side; border of pronotum with lateral expansions; hind trochanter without setae; ely-



Figs. 33–42. *Broscus cephalotes*. (**33**) Head and prothorax; (**34**) mouthparts, ventral view; (**35**) ligula; (**36**) left paramere; (**37**) right paramere; (**38**) median lobe; (**39**) base of median lobe, dorsal view; (**40**) sclerite X, dorsal view; (**41**) sclerite X, lateral view; (**42**) female genital tract, ventral view. See appendix 2 for abbreviations.

tra with supernumerary punctures; striae interruptes; fore and middle tarsomeres of males without adhesive vestiture . . . . . *Craspedonotus*

- Labial submentum with two or more setae on each side; border of pronotum without lateral expansions; hind trochanter with setae; elytra, if striate, with eight regular striae; fore and middle tarsomeres of males with adhesive vestiture 8

8(7). Temporal ridge complete; pronotum with a narrow lateral bead (fig. 33) . . . *Broscus*

- Temporal ridge obsolete, distinct only at the apical region; pronotum without lateral bead (fig. 93) . . . . . *Broscosoma*

Broscus Panzer, 1813

Figures 33–42

Cephalotes Bonelli, 1810: Tabula Synoptica (junior homonym of *Cephalotes* Latreille, 1802).
Broscus Panzer, 1813: 62 (replacement name for *Cephalotes* Bonelli 1810). Putzeys, 1868: 307. Csiki, 1928: 8. Andrewes, 1935: 33.
Pseudocupis Voet, 1769: 6.

TYPE SPECIES (by subsequent monotypy in Panzer, 1813: 62): *Carabus cephalotes* Linné, 1758.

DIAGNOSIS: Maxillary eustipes with two

basal setae. Mentum tooth simple, glossal sclerite bisetose, without longitudinal carina.

REMARKS: The genus has 22 species. Several subgenera have been proposed, but they are not considered here.

DESCRIPTION: External morphology (figs. 33–35): Head with one supraorbital seta over each eye; temporal ridge complete; antenna with antennomeres 1 and 2 glabrous; 3 with apical ring of setae; 4 with apical ring of setae or setose on apical half; 5–11 setose throughout. Mandibles each with scrobal setae. Maxillar eustipes with two basal setae. Labium with two to six setae on submentum; tooth of mentum simple (in some species with a slightly bifid apex) (fig. 34); prementum with glossal sclerite bisetose apically (fig. 35), ventral surface without longitudinal carina. Pronotum constricted apically, with two setae each side. Elytron with parascutellar striole joined to the apical portion of stria 1; parascutellar setae present, on basal portion of second stria; lateral umbilical series with 5 to 11 setae. Foreleg with trochanter having one or two setae; male with foretarsomeres 1–3 with adhesive vestiture of articulosetae ventrally; middle tarsomeres without it.

Male genitalia (figs. 36–41): Sternum 9 with sclerotized ring complete, with lateral margins narrow. Median lobe with dorsal surface sclerotized on the basal third and basal orifice partially open dorsally (fig. 39, bo). Internal sac with sclerite X broad (figs. 40–41), with central constriction (fig. 41, c) and lateroapical symmetric projections upturned; apical plate of long spiculae and without tooth (fig. 38, ap). Left paramere with few setae apically (fig. 36); right paramere setose on apical third (fig. 37).

Female genital tract (fig. 42): Rami of gonocoxite 9 long. Subgonocoxite 9 long, with internal and external rows of ensiform setae. Nematiform setae of subapical setose organ present. Spermatheca long and thin (fig. 42), entering apical region bursa of copulatrix independently from median oviduct; helminthoid sclerite thin and long (fig. 42, hs); bursa copulatrix with accessory gland near spermatheca with basal sclerite U-shaped; with sclerite on the base of oviduct.

LARVAE: The larva of *B. cephalotes* was described by Luff (1978) and Sharova and Makarov (1985). The latter authors described two additional subspecies of *B. cephalotes* and the larva of *B. punctatus*.

HABITAT: *Broscus cephalotes* is very common in dunes along the seacoast in France (Jeannel, 1941) and British Isles (Lindroth, 1974), and also recently *B. cephalotes* was found in sand beaches in eastern Canada (Larochelle and Larivière, 1989). *Broscus semistriatus* occurs in the mountain steppes of the Caucasus. It lives in the mesophytic steppe in open lands of low mountains and steppe hills (Sigida, 1993).

GEOGRAPHICAL DISTRIBUTION: The genus ranges from Spain (including the Canary Island) to central and north Europe, Asia (Arabia, China, India, Iraq, Iran, Tibet, Turquestan, Turkey), north Africa (Algeria, Egypt, and Tunisia), and recently it was introduced in North America, in the form of *B. cephalotes* (Bousquet and Larochelle, 1993). *Broscus glaber* is cited from Mexico (as *Broscus basalis*, junior synonym), but this record must be erroneous.

MATERIAL EXAMINED: *Broscus cephalotes cephalotes* (AMNH, CUIC, MCZ, USNM); *B. cephalotes asiaticus* (AMNH, CUIC); *B. davidianus* (MCZ); *B. laevigatus* (CUIC); *B. nobilis* (CUIC); *B. politus* (CUIC); *B. przewalskyii* (MCZ); *B. punctatus* (CUIC).

Craspedonotus Schauman, 1863

Figures 43–50

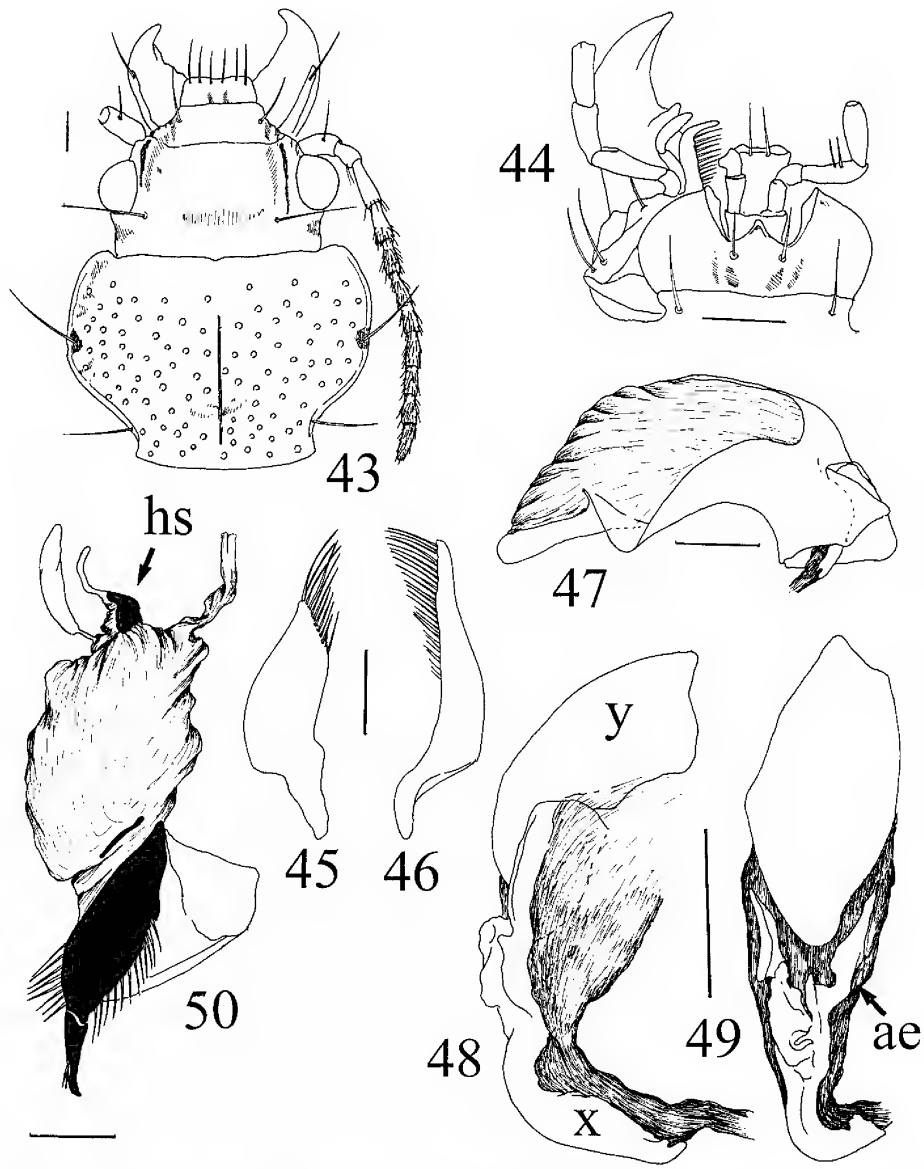
Craspedonotus Schauman, 1863: 86. Putzeys, 1868: 314. Csiki, 1928: 11. Andrewes, 1935: 39.

Pseudobroscus Semenov, 1888: 248 (type species: *Pseudobroscus leucocnemis* Semenov 1888 by monotypy). Semenov, 1899: 41.

TYPE SPECIES (by monotypy): *Craspedonotus tibialis* Schauman, 1863.

DIAGNOSIS: Maxillary eustipes with two basal setae. Mentum tooth simple, glossal sclerite bisetose, without longitudinal carina. Species of *Craspedonotus* are distinguished from other Broscina genera by having elytra and pronotum with supernumerary setae.

DESCRIPTION: External morphology (figs. 43–44): Head with one supraorbital seta over each eye; temporal ridge complete; antenna with antennomeres 1 and 2 glabrous, 3 with apical ring, 4 setose on apical half; 5–11 se-



Figs. 43–50. *Craspedonotus tibialis*. (**43**) Head and prothorax; (**44**) mouthparts, ventral view; (**45**) left paramere; (**46**) right paramere; (**47**) median lobe lateral view; (**48**) sclerite X, dorsal view; (**49**) sclerite X, lateral view; (**50**) female genital tract, ventral view. See appendix 2 for abbreviations.

tose throughout. Mandibles each with scrobal setae. Maxillar eustipes with two basal setae. Labium with submentum bisetose; tooth mentum simple (fig. 44); prementum with glossal sclerite bisetose apically, ventral surface without longitudinal carina. Pronotum constricted apically, with two setae each side. Elytron with parascutellar striole isolated from the apical portion of stria 1; parascutellar setae present, on basal portion of second stria; lateral umbilical series with three to five setae. Foreleg with trochanter with one seta; fore and middle tarsomeres of male without adhesive vestiture.

Male genitalia (figs. 45–49): Sternum 9 with sclerotized ring complete, with lateral margins narrow. Median lobe with dorsal surface sclerotized and basal orifice partially

open dorsally (fig. 47). Internal sac with sclerite X broad and curved (figs. 48–49, X), with central constriction and lateroapical symmetric projections upturned (figs. 49, ae); apical plate of long spiculae and without tooth. Left and right parameres setiferous apically, along inner margins. (figs. 45–46).

Female genital tract (fig. 50): Rami of gonocoxite 9 long; subgonocoxite 9 long, with internal and external rows of ensiform setae. Nematiform setae of subapical setose organ present. Spermatheca short and thin, entering apical region bursa copulatrix independently from median oviduct; helminthoid sclerite broad and short; bursa copulatrix with accessory gland near spermatheca with broad basal sclerite U-shaped. With sclerite on base of oviduct.

GEOGRAPHICAL DISTRIBUTION: The three species of *Craspedonotus* occur in Asia (north and central China, Japan, Korea, Turkestan, Himalayas, and Siberia—southern parts of the Maritime Territory).

EXAMINED: *Craspedonotus tibialis* (CUIC, MCZ, USNM); *C. himalayanus* (MCZ); *C. margellanicus* (MCZ).

Chaetobroscus Semenov, 1899

Figures 51–60

Chaetobroscus Semenov, 1899: 44. Csiki, 1928: 8. Andrewes 1935: 42. Dostal, 1984: 134.

Chaetobroscus (Morvanobroscus) Dostal, 1984: 134 (type species *Chaetobroscus bhutanensis* Morvan, 1980 by original designation).

TYPE SPECIES (by subsequent monotypy in Semenov, 1899): *Broscus anomalus* Chaudoir, 1878.

DIAGNOSIS: Maxillary eustipes with two basal setae. Mentum tooth simple, glossal sclerite bisetose, without longitudinal carina. *Chaetobroscus* is recognized, from other Broscina genera, by the number of supraorbital setae and lateral setae of pronotum.

DESCRIPTION: External morphology (figs. 51–52): Head with three to four supraorbital setae over each eye; temporal ridge almost complete; antenna with antennomeres 1 and 2 glabrous, 3 with apical ring; 4 setose on apical half, 5–11 setose throughout. Mandibles each with scrobal setae. Maxillar eustipes with two basal setae. Labium with six to eight setae on the submentum; tooth of mentum simple (fig. 52); prementum with glossal sclerite bisetose apically, ventral surface without longitudinal carina. Pronotum constricted apically (fig. 51), with seven or eight setae each side. Elytron with parascutellar striole joined to the apical portion of stria 1; parascutellar setae absent; lateral umbilical series with 9–12 setae. Foreleg with trochanter having one seta; male with foretarsomeres 1–2 with adhesive vestiture ventrally, middle tarsomeres without it.

Male genitalia (figs. 53–59): Sternum 9 with sclerotized ring complete, with lateral margins narrow. Median lobe with dorsal surface sclerotized and basal orifice partially open dorsally (fig. 55, bo). Internal sac with sclerite X broad (figs. 58–59), not curved, with central constriction (fig. 58, c) and lateroapical symmetric projections upturned (fig. 59, ae); apical plate of long spiculae (fig. 57, ap), without tooth. Left and right parameres with a row of setae on apical half (figs. 53-54).

Female genital tract (fig. 60): Rami of gonocoxite 9 short. Nematiform setae of subapical setose organ absent. Spermatheca short and thin, entering apical region bursa copulatrix independently from median oviduct; helminthoid sclerite broad and short (fig. 50, hs); bursa copulatrix with accessory gland near spermatheca, with a basal sclerite U-shaped; with sclerite on the base of oviduct.

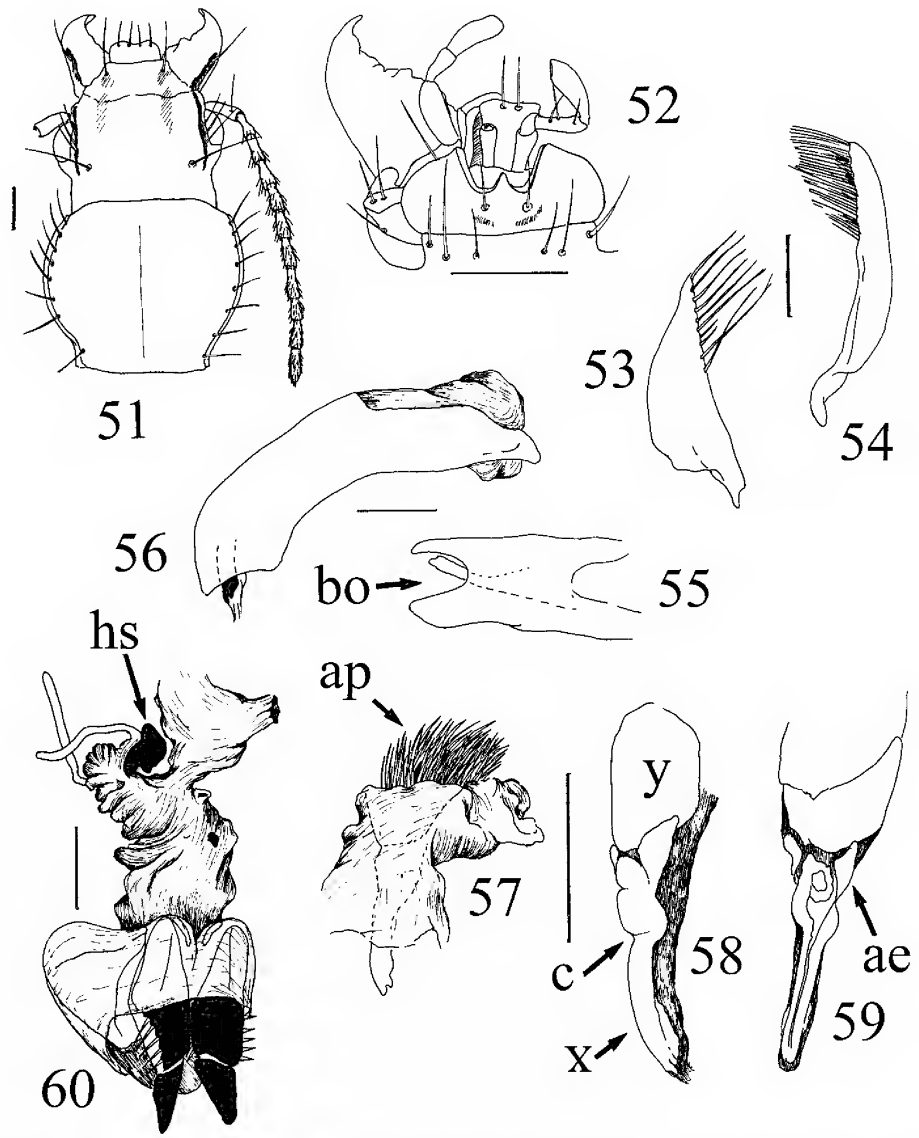
GEOGRAPHICAL DISTRIBUTION: The three species of *Chaetobroscus* occur in the northern part of the Oriental region, on the slopes of the Himalayas (Bhutan and India) (Dostal, 1984).

MATERIAL EXAMINED: *Chaetobroscus anomalus* (USNM).

REMARKS: This genus has three species, grouped in two subgenera (Dostal, 1984).

KEY TO SUBGENERA OF *CHAETOBROSCUS*

1. Anal sternum bisetose at each side in males and females; elytra matte, with striae .... *Chaetobroscus* s. s.
- Anal sternum with one seta at each side in male, with two in females. Elytra smooth, without impressed striae .... *Morvanobroscus*



Figs. 51–60. *Chaetobroscus anomalus*. (**51**) Head and prothorax; (**52**) mouthparts, ventral view; (**53**) left paramere; (**54**) right paramere; (**55**) base of median lobe, dorsal view; (**56**) median lobe; (**57**) apical plate; (**58**) sclerite X, dorsal view; (**59**) sclerite X, lateral view; (**60**) female genital tract, ventral view. See appendix 2 for abbreviations.

Zacotus LeConte, 1869

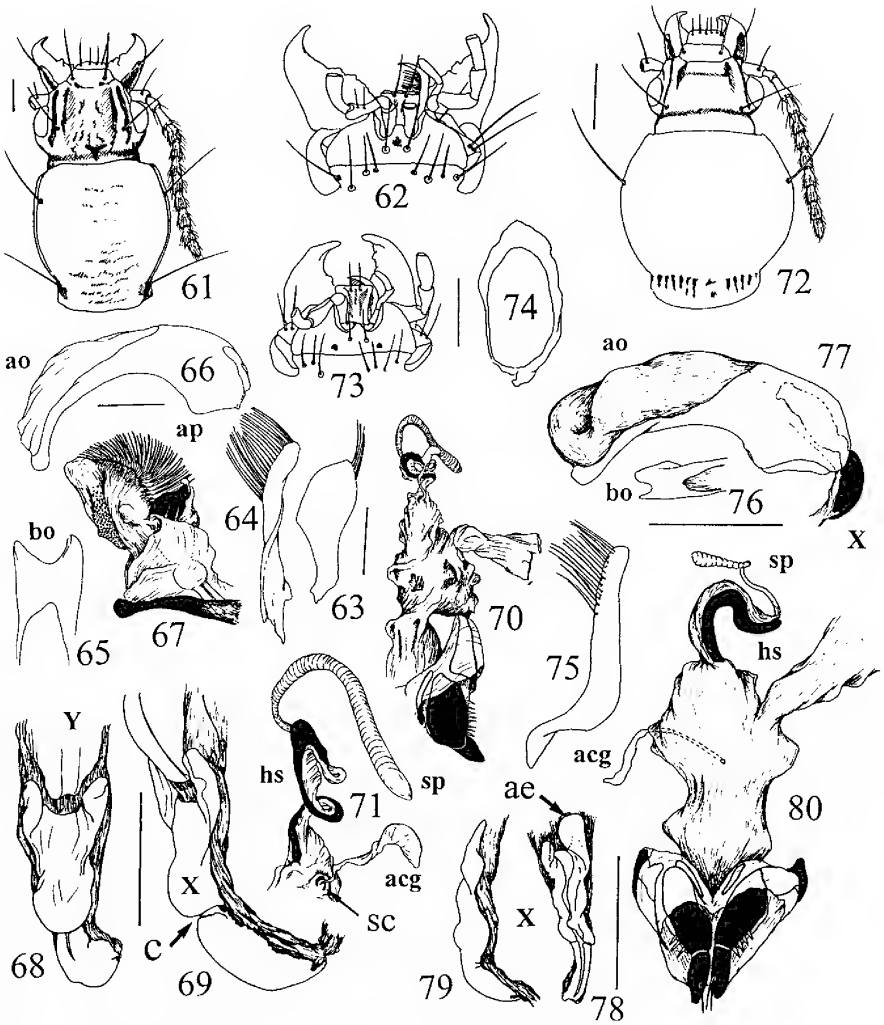
Figures 61–71

Zacotus LeConte, 1869: 373. LeConte and Horn, 1883: 49. Lindroth, 1961b: 172.

TYPE SPECIES (by monotypy): *Zacotus matthewsii* LeConte, 1869.

DIAGNOSIS: Ventral surface of head with two deep, transverse grooves on each side of gula; submentum with 8 to 10 setae.

DESCRIPTION: External morphology (figs. 61–62): Head with one supraorbital seta over each eye; temporal ridge distinct at the apical region; antenna with antennomeres 1 and 2 glabrous, 3–4 only with apical ring of setae; 5–11 setose throughout. Ventral surface of head with two deep, transverse grooves on either side of gula. Mandibles with or without scrobal setae. Maxillar eustipes with two basal setae. Labium with 8–10 setae on sub-



Figs. 61–80. *Zacotus* and *Miscodera*. (**61–71**) *Zacotus matthewsii*: (**61**) Head and prothorax; (**62**) mouthparts, ventral view; (**63**) left paramere; (**64**) right paramere; (**65**) base of median lobe, dorsal view; (**66**) median lobe; (**67**) apical plate; (**68**) sclerite X, dorsal view; (**69**) sclerite X, lateral view; (**70**) female genital tract lateral view; (**71**) spermatheca, helminthoid sclerite. (**72–80**) *Miscodera arctica*: (**72**) Head and prothorax; (**73**) mouthparts, ventral view; (**74**) sternum 9; (**75**) left paramere; (**76**) base of median lobe, dorsal view; (**77**) median lobe; (**78**) sclerite X, dorsal view; (**79**) sclerite X, lateral view; (**80**) female genital tract, ventral view. See appendix 2 for abbreviations.

mentum; mentum with ventral surface almost plane; tooth of mentum simple; prementum with glossal sclerite bisetose apically, ventral surface without longitudinal carina. Pronotum constricted apically, with two setae each side (fig. 61). Elytron with parascutellar striole isolated from apical portion of stria 1; parascutellar setae present on basal portion of second stria; lateral umbilical series with 5–12 setae. Foreleg with trochanter bisetose; male with foretarsomeres 1–3 and middle tarsomeres 1–2 with adhesive vestiture of articulosetae ventrally.

Male genitalia (figs. 63–69): Sternum 9 with sclerotized ring complete with lateral margins narrow. Median lobe with dorsal surface sclerotized on the basal third (fig. 66) and basal orifice partially open dorsally (fig. 65, bo). Internal sac with sclerite X broad and curved (figs. 68–69, X), with central

constriction (fig. 69) and lateroapical symmetric projections; apical plate of long spiculae (fig. 67), without tooth. Left paramere with few setae apically (fig. 63); right paramere setose on apical third (fig. 64).

Female genital tract (figs. 70–71): Rami of gonocoxite 9 long. Nematiform setae of subapical setose organ present. Spermatheca long and thin (fig. 71, sp), entering the apical region bursa copulatrix independently from median oviduct; helminthoid sclerite long and spiraled (fig. 71, hs); bursa copulatrix with accessory gland near the spermatheca (fig. 71, acg); in the base of the gland there is an U-shaped sclerite (fig. 71); with sclerite on the base of oviduct.

HABITAT: The species of this genus inhabits the forest of the Northwest Pacific (Hatch and Fender, 1944), in or at the margin of high, dense coniferous forest (*Abies grandis*, *Thuja plicata*) (Lindroth, 1961b).

GEOGRAPHICAL DISTRIBUTION: The genus *Zacotus* occurs in North America, in USA and Canada, ranging from northern California to southern Alaska (Ball, 1956).

MATERIAL EXAMINED: *Zacotus matthewsii* (AMNH, CUIC, MCZ, USNM).

REMARKS: The single species of *Zacotus* varies geographically in color (Hatch and Fender, 1944; Ball, 1956).

Eobroscus Kryzhanovskij, 1951

Eobroscus Kryzhanovskij, 1951: 538; 1968: 98. Morvan, 1982: 77. Morita, 1990: 155; 1995: 7.
Eobroscus (*Orobroscus*) Morita, 1990: 159 (type species *Eobroscus* (*Orobroscus*) *masumotoi* Morita, 1990 by original designation).

TYPE SPECIES (by original designation): *Eobroscus richteri* Kryzhanovskij, 1951 (junior synonym of *Broscus lutshniki* Roubal, 1928)

DIAGNOSIS: Ventral surface of head with two deep, transverse grooves on each side of gula; submentum with six setae.

DESCRIPTION: External morphology: Head with one supraorbital seta over each eye. Head with a deep transverse sulcus on neck constriction; antenna with antennomeres 1–2 glabrous, 3 with apical ring of setae, 4 setose on apical third; 5–11 setose throughout; ventral surface of head with two deep, transverse grooves at either side of the gula. Mandibles each with or without scrobal setae. Maxillar eustipes with two basal setae. Labium with six to eight setae on submentum; mentum with ventral surface almost plain; tooth of mentum simple, very slightly emarginate or widely rounded; prementum with glossal sclerite bisetose, ventral surface without longitudinal carina. Pronotum constricted apically, with two setae each side. Elytron with parascutellar striole joined to the apical portion of stria 1; parascutellar setae present, on basal portion of second stria; lateral umbilical series with three setae. Male foretarsomeres 1–3 or 1–2 and middle tarsomeres 1–2 with adhesive vestiture of articulosetae ventrally.

Male genitalia: Median lobe with dorsal surface sclerotized on the basal third and basal orifice partially open dorsally; ventral surface with expansions (wings). Internal sac with sclerite X broad, with a marked constriction in the middle and two symmetric lateroapical projections; apical plate of spiculae without tooth. Left and right parameres setiferous,

HABITAT: The species of this genus live in mountain habitats (Morita, 1990, 1995).

GEOGRAPHICAL DISTRIBUTION: The genus *Eobroscus* occurs in Asia. The subgenus *Eobroscus* has a northern distribution, in Eastern Siberia, Northwestern China, and Japan, whereas the subgenus *Orobroscus* has a southern distribution, in Taiwan, Northern Vietnam, and Buthan.

MATERIAL EXAMINED: *Eobroscus lutshniki* (UASM).

REMARKS: *Eobroscus* has four species grouped in two subgenera (Morita, 1990).

KEY TO SUBGENERA OF *EOBROSCUS*

1. Sternum 7 bisetose in males, with two pairs of setae in females; foretarsomeres 1–3 of male with adhesive vestiture; claw segments longitudinally rugose on dorsal surface ..... *Eobroscus*
1′. Sternum 7 bisetose in both sexes; foretarsomeres 1–2 of male with adhesive vestiture; claw segments smooth on the dorsal surface ..... *Orobroscus*

Miscodera Eschscholtz, 1830

Figures 72–80

Miscodera Eschscholtz, 1830: 63. Putzeys, 1868: 354. Csiki, 1928: 12. Lindroth, 1961a: 145; 1961b: 170.

Leiochiton Curtis, 1831: 346 (type species *Scarites arcticus* Paykull, 1798, by original designation).
Oncoderus Stephens, 1832: 377.

TYPE SPECIES (by monotypy): *Scarites arcticus* Paykull, 1798.

DIAGNOSIS: *Miscodera* is distinguished from all Broscina genera in the following combination of characters: pronotum with one seta each side and without lateral bead, and two deep foveae on mentum.

DESCRIPTION: External morphology (figs. 72–73): Head with one supraorbital seta over each eye; head with a broad transverse impression behind eyes (fig. 72); temporal ridge complete; antenna with antennomeres 1–2 glabrous, 3–4 with apical ring of setae. Mandibles each with scrobal setae. Maxillar eustipes with two basal setae. Labium with seven or eight setae on submentum; mentum with two rounded paramedian foveae and a simple tooth; prementum with glossal sclerite bisetose apically, ventral surface without longitudinal carina. Pronotum constricted apically, with one setae each side and without lateral bead. Elytron with striole joined to the apical portion of stria 1; parascutellar setae present on basal portion of second stria; lateral umbilical series with three setae. Foreleg with trochanter having one seta; male with foretarsomeres 1–3 and middle tarsomeres 1–2 with adhesive vestiture of articulosetae ventrally.

Male genitalia (figs. 74–79): Sternum 9 with sclerotized ring complete, with lateral margins narrow (fig. 74). Median lobe with dorsal surface sclerotized on the basal third (fig. 77) and basal orifice dorsally open (fig. 76, bo). Internal sac with sclerite X broad and curved, with lateroapical asymmetric upturned projections (figs. 78–79); apical plate of spiculae, without tooth. Left paramere setose on apical third (fig. 75).

Female genital tract (fig. 80): Rami of gonocoxite 9 long and thin. Nematiform setae of subapical setose organ present. Spermatheca long and thin (fig. 80, sp), entering the apical region bursa copulatrix independently from median oviduct; helminthoid sclerite thin and long, curved (fig. 80, hs); bursa copulatrix with accessory gland in central region, without basal sclerite; with sclerite on the base of oviduct.

LARVAE: The larval instars of *Miscodera arctica* were described by Andersen (1968) and Luff (1978).

HABITAT: *Miscodera arctica* is a xerophilous species, occurring on sandy moraines with mosses or lichens and few trees (Lindroth, 1961b).

GEOGRAPHICAL DISTRIBUTION: The genus *Miscodera* is Holarctic, occurring in North America (USA and Canada), north of Europe (Finland, Sweden, Norway, Denmark, north Germany, and Russia), and Asia (Siberia).

MATERIAL EXAMINED: *Miscodera arctica* (AMNH, CUIC, MCZ, USNM).

Broscodera Lindroth, 1961

Figures 81–92

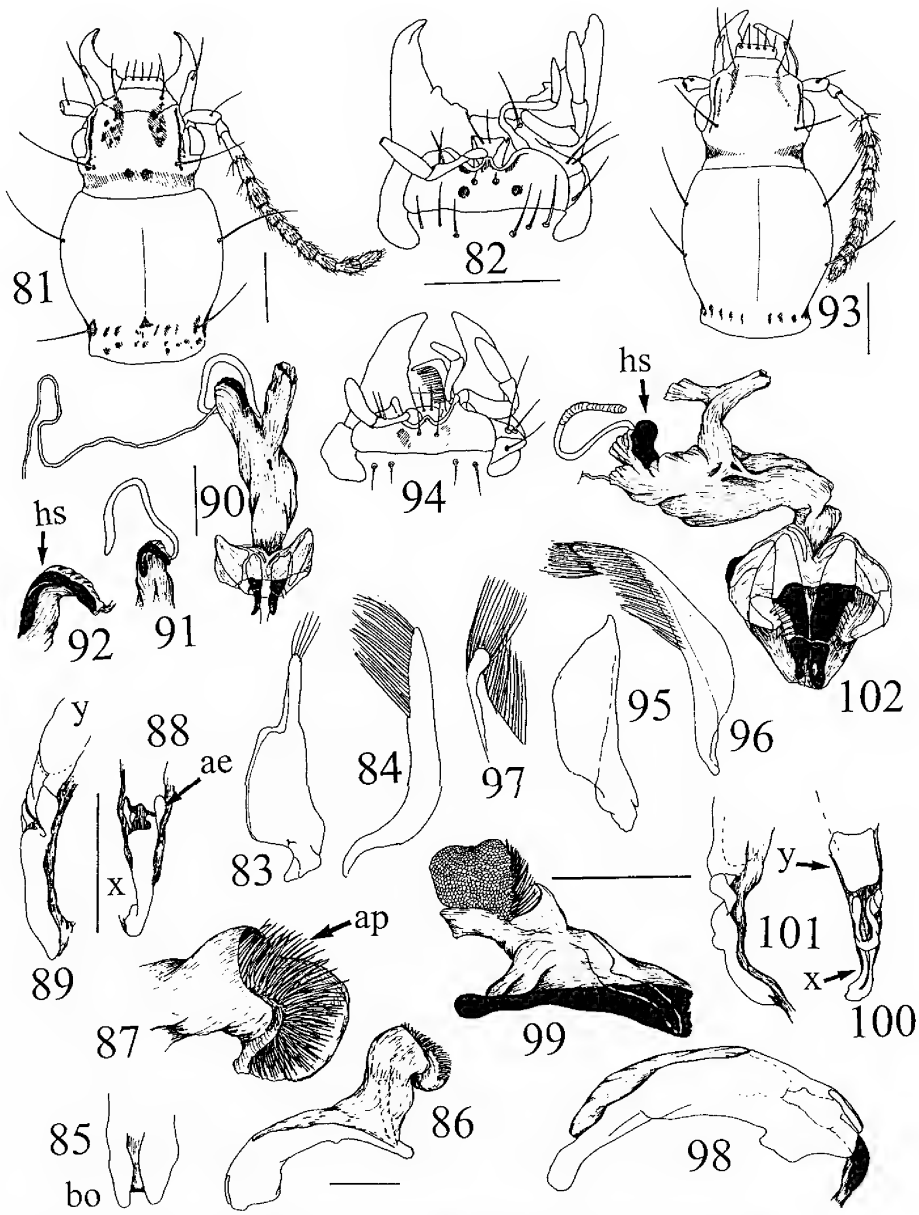
Broscodera Lindroth, 1961a: 150. Lindroth, 1961b: 171.

TYPE SPECIES (by original designation): *Miscodera insignis* Mannerheim, 1852.

DIAGNOSIS: *Broscodera* differs from related Broscina genera by the combination of two characters: absence of parascutellar seta and head without ventral grooves.

DESCRIPTION: External morphology (figs. 81–82): Head with one supraorbital seta over each eye; temporal ridge complete; antenna with antennomeres 1 and 2 glabrous, 3 with apical ring, 4 setose on apical third; 5–11 setose throughout. Mandibles each with scrobal setae. Maxillar eustipes with two or three basal setae. Labium with six setae on submentum; ventral surface of mentum with a deep paramedian circular impression (fig. 82), with tooth simple; prementum with glossal sclerite bisetose apically, ventral surface without longitudinal carina. Pronotum constricted apically, with two setae each side. Elytron with parascutellar striole joined to the apical portion of stria 1; parascutellar setae present, on basal portion of second stria; lateral umbilical series with three setae. Foreleg with trochanter bisetose; male with foretarsomeres 1–3 and middle tarsomeres 1–2 with adhesive vestiture of articulosetae ventrally.

Male genitalia (figs. 83–89): Sternum 9 with sclerotized ring complete, with lateral margins narrow. Median lobe with dorsal surface of the median lobe sclerotized on the basal third (fig. 86), and basal orifice par-



Figs. 81–102. *Broscodera* and *Broscosoma*. **81–92** *Broscodera insignis*: (**81**) head and prothorax; (**82**) mouthparts, ventral view; (**83**) left paramere; (**84**) right paramere; (**85**) base of median lobe, dorsal view; (**86**) median lobe; (**87**) apical plate; (**88**) sclerite X, dorsal view; (**89**) sclerite X, lateral view; (**90**) female genital tract, ventral view; (**91, 92**), spermatheca and helminthoid sclerite. **93–102** *Broscosoma baldense*: (**93**) head and prothorax; (**94**) mouthparts, ventral view; (**95**) left paramere; (**96, 97**), right paramere; (**98**) median lobe; (**99**) apical plate; (**100**) sclerite X, dorsal view; (**101**) sclerite X, lateral view; (**102**) female genital tract, ventral view. See appendix 2 for abbreviations.

tially open dorsally (fig. 85, bo). Internal sac with sclerite X broad (figs. 88–89), with lateroapical asymmetric projections upturned (figs. 88–89); apical plate of long spiculae, without tooth (fig. 87, ap). Left paramere with few setae apically (fig. 83), right paramere setose on apical third (fig. 84).

Female genital tract (figs. 90–92): Rami of

gonocoxite 9 long and thin. Nematiform setae of subapical setose organ present. Spermatheca long and thin (fig. 91), entering the apical region bursa copulatrix independently from median oviduct; helminthoid sclerite thin and long, curved (figs. 91–92, hs); bursa copulatrix with accessory gland near the spermatheca, without basal sclerite; with sclerite on the base of oviduct.

HABITAT: Lindroth (1961b) pointed out that some specimens were found on a steep mountain slope, near the forest limit.

GEOGRAPHICAL DISTRIBUTION: The monospecific genus *Broscodera* occurs in North America, in USA (Alaska, British Columbia, Oregon, Washington, and Wyoming) and Canada.

MATERIAL EXAMINED: *Broscodera insignis* (AMNH, IADIZA).

Broscosoma Rosenhauer, 1846

Figures 93–102

Broscosoma Rosenhauer, 1846: 1. Putzeys, 1846: 1; 1868: 353. Semenov, 1900: 74. Csiki, 1928: 12. Andrewes 1935: 44. Lindroth, 1961a: 146. TYPE SPECIES (by monotypy): *Broscosoma baldense* Rosenhauer, 1846.

DIAGNOSIS: *Broscosoma* together with *Miscodera* are the only Broscina genera without lateral bead in the pronotum. It differs from *Miscodera* in lacking the foveae of mentum.

DESCRIPTION: External morphology (figs. 93–94): Head with one supraorbital seta over each eye; temporal ridge indistinct, distinct at the apical region; antenna with antennomeres 1 and 2 glabrous, 3 with apical ring; 4 setose on apical third; 5–11 setose throughout. Mandibles each with scrobal setae. Maxillar eustipes with two basal setae. Labium with 4–6 setae on submentum; tooth of mentum simple; prementum with glossal sclerite bisetose, ventral surface without longitudinal carina. Pronotum constricted apically (fig. 93), with one or two setae each side, and without lateral bead. Elytron with parascutellar striole joined to apical portion of stria 1; parascutellar setae present, on basal portion of second stria or absent (in *B. gracile*); lateral umbilical series with three or four setae. Foreleg with trochanter with one or two setae; male foretarsomeres 1–3 and middle tarsomeres 1–2 with adhesive vestiture of articulosetae ventrally.

Male genitalia (figs. 95–101): Sternum 9 with sclerotized ring complete and lateral margins narrow. Median lobe with dorsal surface sclerotized on the basal third and basal orifice partially open dorsally (fig. 98). Internal sac with sclerite X broad with lateroapical asymmetric projections upturned (figs. 100–101); apical plate of long spiculae, without tooth (fig. 99). Left paramere asetose (*B. baldense*, fig. 95) or setose (*B. deuvi*, *B. semenovi*, *B. convexum*); right paramere setose on apical half, with apex curved (figs. 96–97).

Female genital tract (fig. 102): Rami of gonocoxite 9 long. Nematiform setae of subapical setose organ present. Spermatheca long and thin (fig. 102), entering the apical region bursa copulatrix independently from median oviduct; helminthoid sclerite broad and short (fig. 102, hs); accessory gland near the spermatheca, without basal sclerite; with sclerite on the base of oviduct.

HABITAT: Most of the species are endemic in some valleys (Deuve, 1983; Belousov and Katayev, 1990), whereas some species are widespread, like *Broscosoma ribbei* that occurs between 3000 and 4000 m in the wet forest of Nepal and Sikkim. *Broscosoma semenovi* occurs in the lower alpine zones of the Caucasus (Belousov and Katayev, 1990), and constitutes an endemic species on the slope of the craggy mountains (Sigida, 1993). *B. schawalleri* Deuve inhabits alpine habitats with *Rhododendron* at 4600 m in Nepal (Deuve, 1990). *Broscosoma moriturum* inhabits alpine zones in China (Semenov, 1900), between 3000 and 4000 m; *B. uenoi* inhabits Taiwan at an altitude of 2320 m (Habu, 1973a).

GEOGRAPHICAL DISTRIBUTION: The genus *Broscosoma* exhibits a markedly discontinuous distribution. One species is from the eastern Alps (*B. baldense*), one from Japan (*B. doenitzi*), one from Taiwan (*B. uenoi*), and one from the Caucasus (*B. semenovi*). The other species are from the Himalaya and Szechwan mountains in China.

REMARKS: This Palearctic genus has 15 species with little morphological variation among them (Deuve, 1983).

MATERIAL EXAMINED: *B. baldense* (USNM,

CUIC); *B. ribbei* (USNM); and *B. doenitzi* (USNM).

Sinobrosculus Deuve, 1990

Sinobrosculus Deuve, 1990: 186.

TYPE SPECIES (by original designation): *Sinobrosculus dreuxi* Deuve, 1990.

REMARKS: This genus has a single species not examined herein, but according to Deuve (1990) it has four setae on the mentum, an exclusive character within the Broscina. The original description was based on one female, but it does not include characters of the genitalia.

GEOGRAPHICAL DISTRIBUTION: The genus occurs in Sichuan, China, at 4000 m.

NOTHOBROSCINA, NEW SUBTRIBE

TYPE GENUS: *Nothobroscus* Roig-Juñent and Ball, 1995.

TAXA INCLUDED: The present cladistic analysis agrees with Balls (1956) postulate that the austral genera that have sclerites X and Y form a monophyletic group, but this assemblage is more closely related to the austral Broscini (Barypina and Creobiina) than to the Holarctic genera (Broscina and Axonyina). For this reason, I erect the subtribe Nothobroscina, including the austral genera with sclerites X and Y on the internal sac.

Figure 15 shows five synapomorphies defining Nothobroscina: tooth of mentum bifid at apex (10^3) and mentum with two rounded foveae (12^1), sclerotized ring of sternum 9 complete and wide (50^0), sclerite X broad with central constriction and without lateroapical projections (59^2), accessory gland of bursa copulatrix far off the spermatheca (65^2), and helminthoid sclerite broad and short (73^2). Some of these characters revert within Nothobroscina, except the apex of mentum tooth, form of internal sac sclerite X of male, and the shape of sclerotized ring of sternum 9. Within Nothobroscina, *Diglymma* appears as the most plesiomorphic genus, as pointed out by Ball (1956). The sister group of *Diglymma* is formed by two monophyletic groups, one including *Eurylychnus* and *Nothobroscus*, characterized by the presence of narrow and curved frontal sulcus (7^2), and the other including seven genera characterized by the absence of scrobal seta (8^1), metafemur setae not aligned (46^1), and accessory gland of bursa copulatrix near spermatheca (65^1). This latter group includes the genus *Mecodema* (the most diversified genus, with 61 species).

This subtribe comprises 10 genera (only two monospecific) with 92 species that occur in Australia (plus Tasmania), New Zealand, New Caledonia, and southern South America. The nothobroscine species live in different habitats. The species of *Mecodema* mostly inhabit alpine regions in New Zealand, *Brullea* has a psammophilus habitat, and *Nothobroscus* and *Eurylychnus* inhabit *Nothofagus* forest in South America and Australia, respectively.

KEY TO GENERA OF NOTHOBROSCINA

1. Each side of head with a single supraorbital puncture plurisetose; external apex of foretibia expanded; elytra with row of setiferous punctures on 7th interval . . .2
- Each side of head with one or more supraorbital punctures, bearing a single seta; external apex of foretibia not expanded; elytra without row of setiferous punctures on 7th interval 4

2(1). Foretibia wide, markedly expanded at apex; middle and hind tibiae curved and greatly expanded at apex, very punctuated on the outer side . . . . . *Brullea*
- Foretibia thin, with an expansion at apex, middle and hind tibiae not curved and expanded, with few punctures on outer side 3

3(2). Antennomeres 2–10 lacking pubescence except for an apical ring of setae; glossal sclerite with V-shaped posteroapical margin (as *Brullea* in fig. 202) . . . . . *Metaglymma*
- Antennomeres 3–5 with an apical ring of setae and remaining with pubescence all along the surface; glossal sclerite with right posteroapical margin (fig. 177) . . . . . *Mecodema*

4(1). Head with a single supraorbital puncture on each side; mentum with two deep paramedian foveae; almost always with two setae in the eustipes 6
- Head with two or more supraorbital punctures on each side; mentum without fovea; three setae in the eustipes 5

5(4). Prothorax straightly compressed at the apex, second article of the maxillary palp with more than two setae (7–8);

foreleg trochanter with one seta; abdominal sterna smooth ..... *Percosoma*

- Prothorax not compressed at apex, second article of the maxillary palp bisetose; foreleg trochanter bisetose; abdominal sterna with two lateral foveae (in some cases slightly foveated) ..... *Oregus*

6(4). Head with a transverse impression behind eyes, frontal grooves present 7

- Head without a transverse impression behind eyes; frontal grooves absent .... *Percolestus*

7(6). Without parascutellar setae on basal portion of second stria 8

- With parascutellar setae on basal portion of second stria ..... *Diglymma*

8(7). Scrobal mandibles without setae; prothorax with 4–6 setae on each side; parascutellar striole joined to the apical portion of stria 1 ..... *Chylnus*

- Scrobal mandibles with setae; prothorax with 1–3 setae on each side; parascutellar striole joined or isolated from the apical portion of stria 1 9

9(8). Submentum with six setae; prothorax with more than one setae on each side; pronotum rounded, not constricted apically; male foretarsomeres 1–3 with adhesive vestiture ..... *Eurylychnus* (*E. olliffi* group)

- Submentum bisetose; prothorax with one seta on each side; pronotum constricted apically; male foretarsomeres without adhesive vestiture 10

10(9). Parascutellar striole isolated from apical portion of stria 1; abdominal sterna without setae .... *Eurylychnus* (*E. blagravii* group)

- Parascutellar striole joined to the apical portion of stria 1; abdominal sterna with setae ..... *Nothobroscus*

Diglymma Sharp, 1886

Figures 103–112

Diglymma Sharp, 1886: 360. Broun, 1893: 980; 1908: 340. Csiki, 1928: 19. Britton, 1949: 539. Townsend, 1971: 174.

Snofru Broun, 1908: 340 (type species *Snofru aemulator* by monotypy, junior synonym of *Diglymma obtusum*).

TYPE SPECIES (by subsequent designation in Britton, 1949): *Maoria clivinoides* Castelnau, 1867.

DIAGNOSIS: Mentum tooth bifid; eyes not emarginate; one supraorbital seta and without a transverse impression behind eyes; with parascutellar setae.

DESCRIPTION: External morphology (figs. 103–104): Head with one supraorbital puncture bearing a single seta over each eye; temporal ridge almost complete, erased only in the middle, antenna with antennomere 1 and 2 glabrous, 3 with apical ring; 4 setose on apical half; 5–11 setose throughout. Mandibles each with scrobal setae. Maxilla with eustipes with two basal setae. Labium with 2–4 setae on submentum; mentum with two paramedian rounded foveae (fig. 104); tooth of mentum bifid apically; prementum with glossal sclerite bisetose apically, ventral surface keeled longitudinally. Pronotum slightly constricted at apex (fig. 103), with two to four setae each side. Elytron with parascutellar striole isolated from the apical portion of stria 1; parascutellar setae present, on basal portion of second stria; 7th interval lacking setae; lateral umbilical series with nine setae. Foreleg with trochanter having one seta; foretibia not prolonged externally to a point at apex; male with foretarsomeres 1-2 with adhesive vestiture of articulosetae, middle tarsomeres without it.

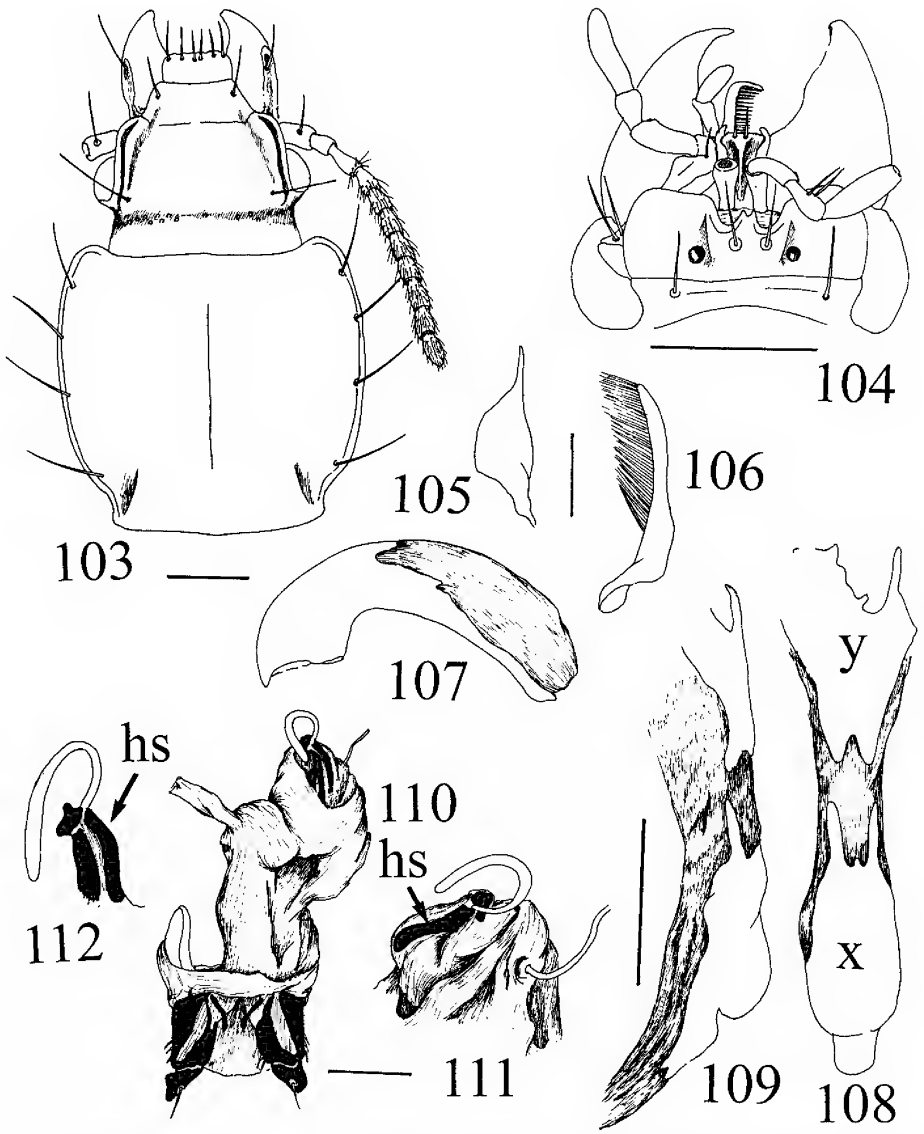
Male genitalia (figs. 105–109): Sternum 9 with sclerotized ring complete with lateral margins wide. Median lobe with dorsal surface sclerotized on basal half (fig. 107) and basal orifice completely closed dorsally. Internal sac with sclerite X broad, without central constriction (figs. 108–109), and without lateroapical upturned projections; apical plate of short spiculae, without tooth. Left paramere asetose (fig. 105); right paramere setose on the two apical thirds (fig. 106).

Female genital tract (figs. 110–112): Rami of gonocoxite 9 long. Subgonocoxite 9 short, with two lateral rows of ensiform setae; gonopod 9 short, nematiform setae of subapical setose organ present. Spermatheca short and thin (fig. 112), entering the apical region bursa copulatrix independently from median oviduct; helminthoid sclerite broad, two times longer than wide (figs. 111–112, hs); bursa copulatrix with accessory gland near the spermatheca, without basal sclerite; with sclerite on the base of oviduct.

LARVAE: The larva of *D. castigatum* is described by Townsend (1971).

HABITAT: *D. castigatum* inhabits subantarctic habitat of the Snares Island.

GEOGRAPHICAL DISTRIBUTION: The four



Figs. 103–112. *Diglymma. Diglymma obtusum*: (**103**) head and prothorax; (**104**) mouthparts ventral view; *Diglymma ovipenne*: (**105**) left paramere; (**106**) right paramere; (**107**) median lobe; (**108**) sclerite X, dorsal view; (**109**) sclerite X, lateral view; *Diglymma obtusum*: (**110**) female genital tract, lateral view; (**111, 112**) spermatheca and helminthoid sclerite. See appendix 2 for abbreviations.

species of *Diglymma* occur in New Zealand, three from the South Island, one of which also occurs in the North Island, and *D. castigatum,* which is endemic from the Snares.

REMARKS: The last revision of this genus was made by Britton (1949) in his studies about the Carabidae of New Zealand. The four species are divided into two very distinct groups based on internal structures of the male genitalia (Townsend, 1971).

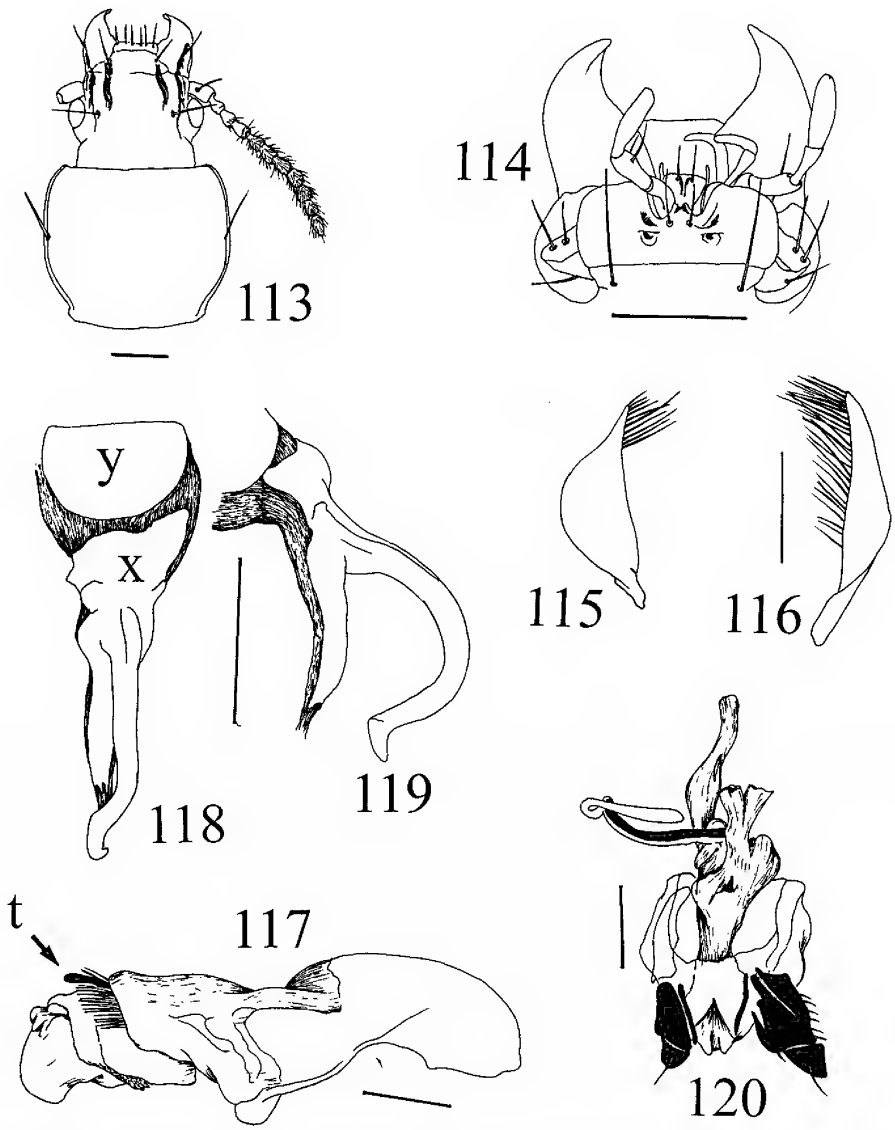
MATERIAL EXAMINED: *Diglymma obtusum* (CUIC); *D. clivinoides* (MCZ).

Nothobroscus Roig-Juñent and Ball, 1995

Figures 113–120

Nothobroscus Roig-Juñent and Ball, 1995: 306.

TYPE SPECIES (by original designation): *Nothobroscus chilensis* Roig-Juñent and Ball, 1995.



Figs. 113–120. *Nothobroscus chilensis*. (**113**) Head and prothorax; (**114**) mouthparts, ventral view; (**115**) left paramere; (**116**) right paramere; (**117**) median lobe; (**118**) sclerite X, dorsal view; (**119**) sclerite X, lateral view; (**120**) female genital tract, lateral view. See appendix 2 for abbreviations.

DIAGNOSIS: This genus is recognized from all the broscine genera by the presence of a dorsal projection of the sclerite X of internal sac.

DESCRIPTION: External morphology (figs. 113–114): Head with one supraorbital puncture bearing a single seta over each eye; a slight transverse impression in the vertex; frontal impressions curved, diverging backward; temporal ridge obsolete on middle; antenna with antennomeres 1 and 2 glabrous, 3–4 with apical ring of setae, 5–11 setose throughout. Mandibles each with scrobal setae. Maxilla with eustipes with two basal setae. Labium with submentum bisetose; mentum with two deep paramedian rounded foveae (fig. 114); tooth of mentum bifid; prementum with glossal sclerite bisetose apically, ventral surface keeled longitudinally. Pronotum slightly constricted at apex (fig. 113), with one setae each side. Elytron with parascutellar striole joined to the apical por-

tion of stria 1; without parascutellar setae on basal portion of second stria; 7th interval lacking setae; lateral umbilical series with 12–17 setae. Foreleg with trochanter bisetose; foretibia not prolonged externally to a point at apex; male with fore and middle tarsomeres without adhesive vestiture.

Male genitalia (figs. 115–117): Sternum 9 with sclerotized ring complete with lateral margins wide. Median lobe with dorsal surface sclerotized on two basal third (fig. 117) and basal orifice completely closed dorsally. Internal sac with sclerite X broad, without lateroapical projections and central constriction (figs. 118–119), with a long and curved dorsal projection; apical plate of long spiculae, with sclerotized tooth (fig. 117, t). Left paramere setiferous on apical third (fig. 115), right paramere setose on the two apical thirds (fig. 116).

Female genital tract (fig. 120): Rami of gonocoxite 9 long. Subgonocoxite 9 short, with one lateral row of ensiform setae; gonopod 9 short, with nematiform setae on subapical setose organ. Spermatheca short and thin, entering the apical region bursa copulatrix independently from median oviduct; helminthoid sclerite thin and long, more than five times longer than wide (fig. 120); bursa copulatrix with accessory gland in central region, without basal sclerite; with sclerite on base of oviduct.

HABITAT: The only known species of *Nothobroscus* occurs in the *Nothofagus* forest, like the species of *Eurylychnus* (Sloane, 1916; Darlington, 1961). Specimens are cited from the *Nothofagus dombeyi* forest, in the Maule region of Chile (Roig-Juñent and Ball, 1995).

GEOGRAPHICAL DISTRIBUTION: Neotropical region, in southern South America (Chile).

MATERIAL EXAMINED: *Nothobroscus chilensis* (USNM, AMNH, IADIZA).

Eurylychnus Bates, 1891

Figures 121–136

Eurylychnus Bates, 1891: 285. Sloane, 1892: 50; 1916: 199. Csiki, 1928: 21. Lawrence et al., 1987: 120.

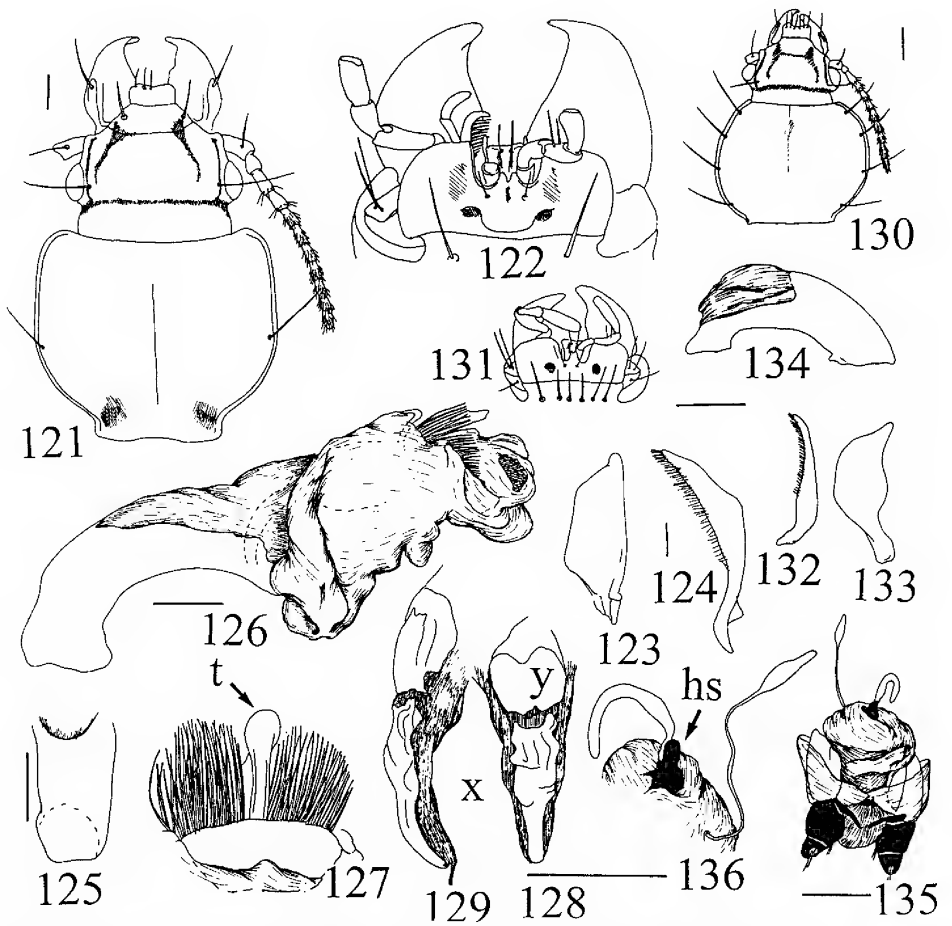
TYPE SPECIES (by monotypy): *Eurylychnus olliffi* Bates, 1891 (= *Maoria dyschiroides* Castelnau, 1868).

DIAGNOSIS: The species of *Eurylychnus* are recognized within Nothobroscina by the following combination of characters: one supraorbital seta; head without transverse impression, without parascutellar seta, mandibular scroba with seta; and submentum with two or six setae.

DESCRIPTION: External morphology (figs. 121–122, 130–131): Head with one supraorbital puncture bearing a single seta over each eye; head with a transverse impression behind the eyes; frontal impressions curved, diverging backward; temporal ridge distinct at the apical region; antenna with antennomeres 1 and 2 glabrous, 3–4 only with apical ring of setae or 4 half setose on apical half, 5–11 setose throughout. Mandibles each with scrobal setae. Maxillary eustipes with two basal setae. Labium with two (fig. 122) to six setae (fig. 132) on submentum; mentum with two rounded paramedian foveae; tooth of mentum bifid apically; prementum with glossal sclerite bisetose apically, ventral surface keeled longitudinally. Pronotum constricted apically (fig. 121) or not (fig. 130), with one (fig. 121) to three setae (fig. 130) each side. Elytron with parascutellar striole joined or isolated from the apical portion of stria 1; parascutellar setae absent; 7th interval lacking setae; lateral umbilical series with 8–11 setae. Foreleg with trochanter having one or two setae; foretibia not prolonged externally to a point at apex; male foretarsomeres 1–2 with or without adhesive vestiture, middle tarsomeres without it.

Male genitalia (figs. 123–129, 132–134): Sternum 9 with sclerotized ring complete with lateral margins wide. Median lobe with dorsal surface sclerotized on basal third (fig. 126) or basal half (fig. 134), and basal orifice completely closed dorsally (fig. 125); without basal keel. Internal sac with sclerite X broad, without central constriction and lateroapical projections (figs. 128–129); apical plate of long spiculae and a central tooth (fig. 127, t). Left paramere asetose (figs. 123, 133); right setose on apical half (figs. 124, 132).

Female genital tract (*E. olliffi*, figs. 135–136): Rami of gonocoxite 9 long and thin. Subgonocoxite 9 short and broad, with two external ensiform setae; gonopod 9 short, nematiform setae of subapical setose organ pre-



Figs. 121–136. *Eurylychnus*. (**121–129**) Group A, *Eurylychnus blagravii*: (**121**) head and prothorax; (**122**) mouthparts, ventral view; (**123**) left paramere; (**124**) right paramere; (**125**) base of median lobe, dorsal view; (**126**) median lobe; (**127**) apical plate; (**128**) sclerite X, dorsal view; (**129**) sclerite X, lateral view; (**130–136**) Group B, *Eurylychnus ollifi*: (**130**) head and prothorax; (**131**) mouthparts, ventral view; (**132**) left paramere; (**133**) right paramere; (**134**) median lobe; (**135**) female genital tract, ventral view; (**136**) spermatheca and accessory gland. See appendix 2 for abbreviations.

sent. Spermatheca short and thin (fig. 136), entering the apical region bursa copulatrix independently from median oviduct; helminthoid sclerite broad and short (fig. 136, hs); bursa copulatrix with accessory gland in the central region without basal sclerite; with sclerite on the base of oviduct.

LARVAE: The larva of *Eurylychnus blagravii* was described by Moore (1964).

HABITAT: Wet forest of Australia and Tasmania (Darlington, 1961), open and tall forest (Lawrence et al., 1987).

GEOGRAPHICAL DISTRIBUTION: The genus *Eurylychnus* occurs in Tasmania, the mountains of southeastern Australia (Victoria and New South Wales), and two isolated species on the Mt. Royal Range and Dorrigo-Ebor plateau. Lawrence et al. (1987) reported the occurrence of the genus in New Caledonia.

REMARKS: This genus has eight species grouped into two very distinct groups. The first group shares some characters with *Diglymma*, and the second with *Nothobroscus*.

KEY TO SPECIES GROUPS OF *EURYLYCHNUS*

1. Submentum with six setae; pronotum with more than one seta each side; pronotum not compressed, rounded; prosternum with a border along anterior margin; male foretarsomeres 1–2 with adhesive vestiture; parascutellar striole

joined to apical portion of stria 1; abdominal sterna with two setae. . . group A (*E. dyschiroides* and *E. femoralis*, plus *E. ovipenne* and *E. victoriae,* not revised).

- Submentum with two setae; pronotum with one seta each side; pronotum compressed; prosternum with a smooth anterior margin; males without adhesive vestiture in foretarsomeres; parascutellar striole isolated from apical portion of stria 1; abdominal sterna without setae . . . . . group B . . (*E. blagravii, E. cylindricus, E. regularis)*

MATERIAL EXAMINED: *Eurylychnus blagravii* (ANIC, CUIC, MCZ); *E. cylindricus* (MCZ); *E. femoralis* (MCZ); *E. dyschiroides* (CUIC, MCZ); and *E. regularis* (MCZ).

Chylnus Sloane, 1920

Figures 137–145

Lychnus Putzeys, 1868: 324; 1873: 317. Sloane, 1892: 56 (type species *Lychnus ater* Putzeys, 1868, by monotypy).

Chylnus Sloane, 1920: 129 (nom. nov. for *Lychnus* Putzeys, 1868). Csiki, 1928: 20. Lawrence et al., 1987: 120.

TYPE SPECIES (by monotypy): *Lychnus ater* Putzeys, 1868.

DIAGNOSIS: *Chylnus*, together with *Percolestus*, are the only genera of Broscini with the spiculae of apical plate fused forming a plate. *Chylnus* differs from *Percolestus* in having a impression behind the eyes and frontal impressions.

DESCRIPTION: External morphology (figs. 137–138): Head with one supraorbital puncture bearing a single seta over each eye; head with a transverse impression behind eyes; frontal impressions curved, diverging backward; temporal ridge distinct at apical region; antenna with antennomeres 1 and 2 glabrous, 3–4 only with apical ring of setae; 5–11 setose throughout. Mandibles without scrobal setae. Maxillary eustipes with two basal setae. Labium with submentum bisetose; mentum with two rounded paramedian foveae; tooth of mentum bifid; prementum with glossal sclerite bisetose apically; ventral surface keeled longitudinally. Pronotum not constricted apically (fig. 137), with four–six setae each side. Elytron with parascutellar striole joined to the apical portion of stria 1; parascutellar setae absent; 7th interval lacking setae; lateral umbilical series with 11–16 setae. Foreleg with trochanter having one seta; foretibia expanded at apex but not externally prolonged; male forefemur expanded at middle; male fore and middle tarsomeres without adhesive vestiture ventrally.

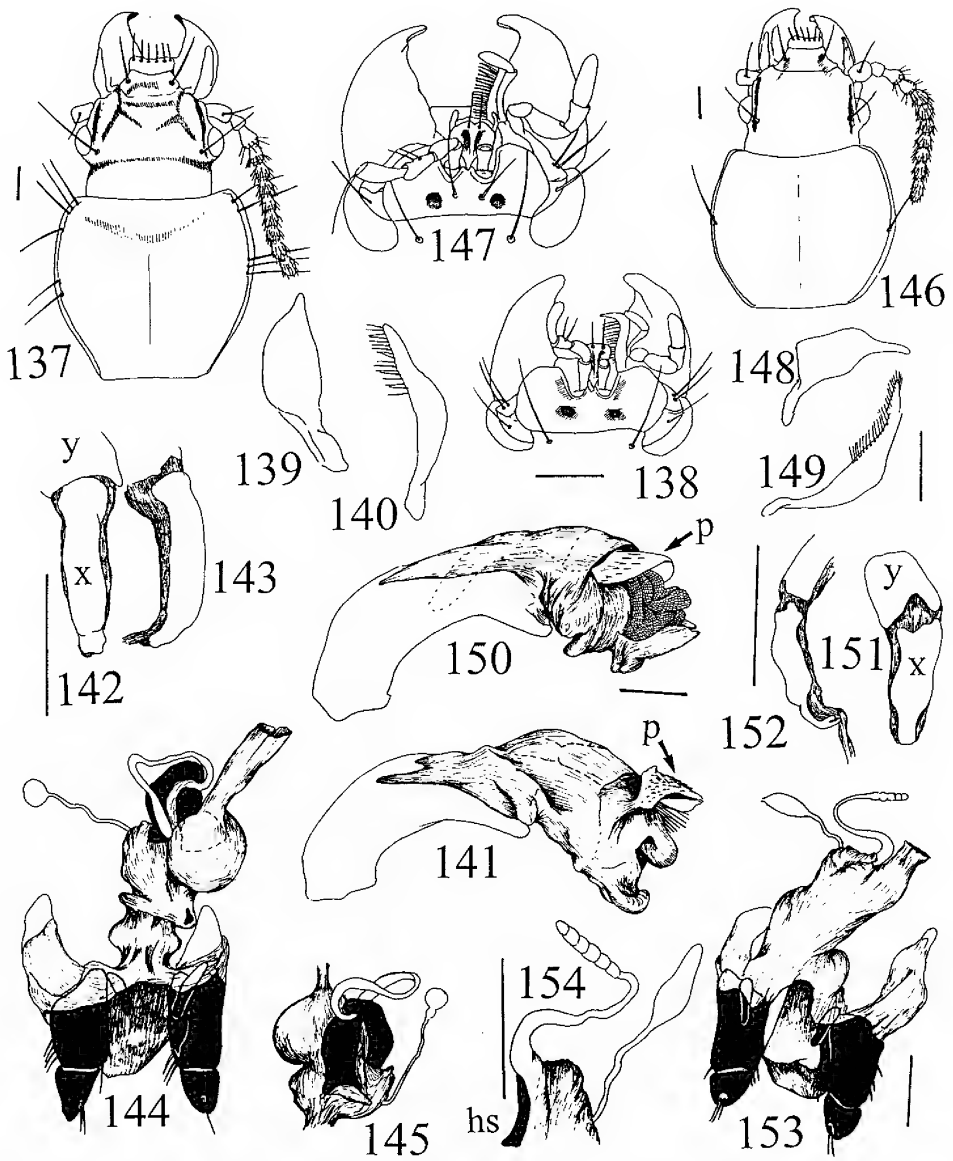
Male genitalia (figs. 139–143): Sternum 9 with sclerotized ring complete with lateral margins wide. Median lobe with dorsal surface sclerotized on basal third (fig. 141) and basal orifice completely closed dorsally; without basal keel. Internal sac with sclerite X broad, without central constriction and lateroapical projections (figs. 142–143); spiculae of apical plate completely fused, forming a plate, without tooth (fig. 141, p). Left paramere asetose (fig. 139); right setose on apical third (fig. 140).

Female genital tract (figs. 144–145): Rami of gonocoxite 9 long. Subgonocoxite 9 short and broad, with external and internal ensiform setae; gonopod 9 short; nematiform setae of subapical setose organ present. Spermatheca long and thin, entering apical region bursa copulatrix independently from median oviduct; helminthoid sclerite broad and divided longitudinally (fig. 145); bursa copulatrix with accessory gland near spermatheca, without basal sclerite (fig. 145); with sclerite on base of oviduct.

HABITAT: *Chylnus ater* is confined to the Tasmanian wet forest (Darlington, 1961). *C. concolor*, *C. montanus*, and *C. substriatus* are reported in tall forest (Lawrence et al., 1987).

GEOGRAPHICAL DISTRIBUTION: The genus occurs in southeastern Australia and Tasmania.

REMARKS: Sloane (1920) reported that this genus included one species from Tasmania. Sloane (1892) stated that the "Victorian (Australian) species of *Percosoma*" are more related to the species of *Chylnus* than to the species of *Percosoma* (*P. carenoides* and *P. sulcipenne* from Tasmania). The study of two species of the Australian group of *Percosoma* supports the conclusion that *P. concolor* Sloane, 1892, *P. montanus* (Castelnau, 1867), and *P. substriatum* Moore, 1960 must be transferred to the genus *Chylnus*. The Australian species of *Percosoma* differ from *P. carenoides* (type species of *Percosoma*) and *P. sulcipenne*, and are related to *Chylnus* in the following: mentum with two rounded



Figs. 137–154. *Chylnus* and *Percolestus*. (**137–145**) *Chylnus ater*: (**137**) head and prothorax; (**138**) mouthparts, ventral view; (**139**) left paramere; (**140**) right paramere; (**141**) median lobe; (**142**) sclerite X, dorsal view; (**143**) sclerite X, lateral view; (**144**), female genital tract, ventral view; (**145**), spermatheca and helminthoid sclerite. (**146–154**) *Percolestus blackburni*: (**146**) head and prothorax; (**147**) mouthparts ventral view; (**148**) left paramere; (**149**) right paramere; (**150**) median lobe; (**151**) sclerite X, dorsal view; (**152**) sclerite X, lateral view; (**153**) female genital tract, ventral view; (**154**) spermatheca and helminthoid sclerite. See appendix 2 for abbreviations.

foveae; eyes rather prominent, with pronounced postocular prominences, almost equal in eye size; head with frontal impressions, a transverse impression across vertex behind eyes; spiculae of apical plate fused; gonopod 9 with nematiform setae on subapical setose organ.

MATERIAL EXAMINED: *Chylnus ater* (ANIC, MCZ); *C. concolor* NEW COMBINATION (MCZ), and *C. substriatum* NEW COM-

BINATION (MCZ). I have not seen *Percosoma montanus* (Castelnau, 1867) but its characters, discussed below, led me to consider it as *Chylnus montanus* NEW COMBINATION.

Percolestus Sloane, 1892

Figures 146–154

Percolestus Sloane, 1892: 54. Csiki, 1928: 20. Lawrence et al., 1987: 121.

TYPE SPECIES (by monotypy): *Percolestus blackburni* Sloane, 1892.

DIAGNOSIS: *Percolestus* and *Chylnus* are the only genera of Broscini with the spiculae of apical plate fused forming a plate. *Percolestus* differs from *Chylnus* in lacking an impression behind eyes and frontal impressions.

DESCRIPTION: External morphology (figs. 146–147): Head with one supraorbital puncture bearing a single seta over each eye; head without a transverse impression behind eyes; without frontal impressions; temporal ridge distinct at apical region; antenna with antennomeres 1 and 2 glabrous, 3–4 only with apical ring of setae; 5–11 setose throughout. Mandibles without scrobal setae. Maxillary eustipes with two basal setae. Labium with submentum bisetose; mentum with two rounded paramedian foveae; tooth of mentum bifid; prementum with glossal sclerite bisetose apically, ventral surface keeled longitudinally. Pronotum not constricted apically (fig. 146), with one seta each side. Elytron with parascutellar striole joined to the apical portion of stria 1; parascutellar setae absent; 7th interval lacking setae; lateral umbilical series with 8–10 setae. Foreleg trochanter with one seta; foretibia not prolonged externally at apex; male fore and middle tarsomeres without adhesive vestiture.

Male genitalia (figs. 148–152): Sternum 9 with sclerotized ring complete and lateral margins wide. Median lobe with dorsal surface sclerotized on basal third (fig. 150) and basal orifice completely closed dorsally, without basal keel. Internal sac with sclerite X broad, without central constriction and lateroapical projections (figs. 151–152); spiculae of apical plate fused forming a plate (fig. 150, p), without tooth. Left paramere asetose (fig. 148); right setose on apical half (fig. 149).

Female genital tract (figs. 153–154): Rami of gonocoxite 9 long. Subgonocoxite 9 short and broad, with external and internal ensiform setae; gonopod 9 short, with nematiform setae on subapical setose organ. Spermatheca short and thin (fig. 154), entering the apical region bursa copulatrix independently from median oviduct; helminthoid sclerite long and thin (fig. 154, hs); bursa copulatrix with accessory gland near spermatheca, without basal sclerite; with sclerite on base of oviduct.

HABITAT: Subalpine areas (Lawrence et al., 1987)

GEOGRAPHICAL DISTRIBUTION: The unique species of *Percolestus* occurs in south Australia (Victoria).

MATERIAL EXAMINED: *Percolestus blackburni* (MCZ).

Oregus Putzeys, 1868

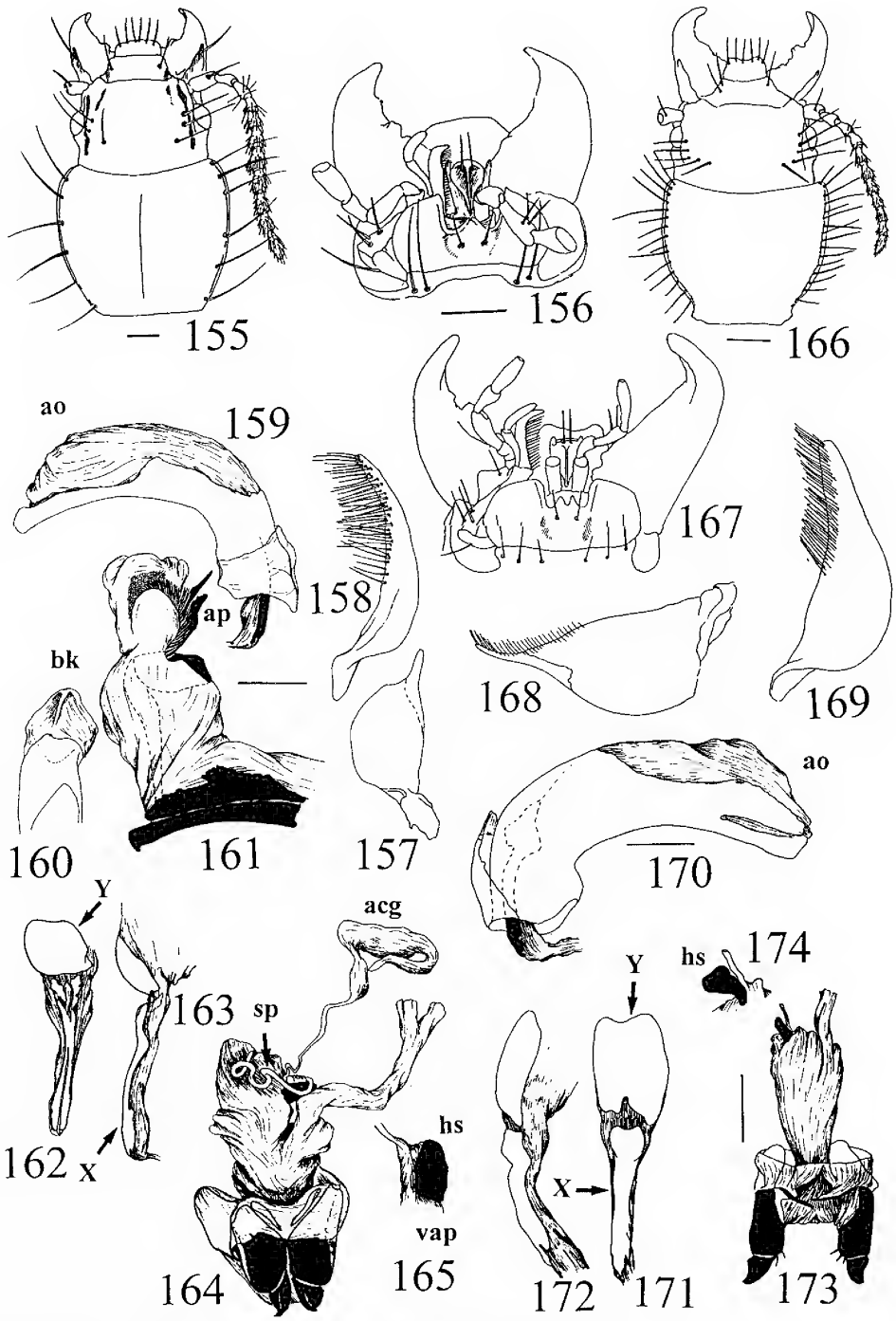
Figures 155–165

Oregus Putzeys, 1868: 326; 1873: 317. Broun, 1880: 13. Csiki, 1928: 19. Britton, 1949: 542.

TYPE SPECIES (by subsequent monotypy in Putzeys, 1868): *Promecoderus aereus* White, 1846.

DIAGNOSIS: *Oregus* is recognized within Nothobroscina by the two supraorbital setae on each side and pronotum with 6–11 setae on each side. The presence of a small basal keel is exclusive of *Oregus* and *Percosoma* within Nothobroscina.

DESCRIPTION: External morphology (figs. 155–156): Head with two single supraorbital punctures on each side, each bearing a seta; vertex with one to five setae on each side; head without a transverse impression behind eyes and frontal impressions; temporal ridge distinct at apical region; antenna with antennomeres 1 and 2 glabrous, 3 with apical ring; 4 pubescent on the apical region; 5–11 setose throughout. Mandibles with or without scrobal setae. Maxillary eustipes with three basal setae. Labium with submentum quadrisetose; mentum ventral surface almost plane; tooth mentum bifid; prementum with glossal sclerite bisetose apically, ventral surface keeled longitudinally. Pronotum not constricted, with 6–11 setae each side. Elytron with parascutellar striole isolated from the apical portion of stria 1; with parascutellar setae on



Figs. 155–174. *Oregus* and *Percosoma*. (**155–165**) *Oregus inaequalis*: (**155**) head and prothorax; (**156**) mouthparts, ventral view; (**157**) left paramere; (**158**) right paramere; (**159**) median lobe; (**160**) base of median lobe; (**161**) internal sac with the apical plate; (**162**) sclerite X, dorsal view; (**163**) sclerite X, lateral view; (**164**) female genital tract, ventral view; (**165**) spermatheca and helminthoid sclerite. (**166–174**) *Percosoma carenoides*: (**166**) head and prothorax; (**167**) mouthparts, ventral view; (**168**) left paramere; (**169**) right paramere; (**170**) median lobe; (**171**) sclerite X, dorsal view; (**172**) sclerite X, lateral view; (**173**) female genital tract, ventral view; (**174**) spermatheca and helminthoid sclerite. See appendix 2 for abbreviations.

basal portion of second stria; 7th interval lacking setae; lateral umbilical series with 11–14 setae, a supernumerary striae placed between striae 7 and 8. Foreleg trochanter with one seta; foretibia not prolonged externally to a point at apex; male fore and middle tarsomeres without adhesive vestiture. Abdominal sterna 5–7 with two slight lateral foveae.

Male genitalia (figs. 157–163): Sternum 9 with sclerotized ring complete with lateral margins wide. Median lobe with dorsal surface sclerotized on basal third (fig. 159) and basal orifice completely closed dorsally (fig. 160); with a small basal keel (figs. 159–160, bk), that is the secondary membrane partially sclerotized. Internal sac with sclerite X elongate, abruptly narrowed, and expanded near insertion of ejaculatory duct at its basal extremity (figs. 162–163); without lateroapical projections; apical plate of long spiculae, with a sclerotized bifid tooth (fig.161, ap). Left paramere asetose (fig. 157); right paramere setose on apical half (fig. 158).

Female genital tract (figs. 164–165): Rami of gonocoxite 9 long. Subgonocoxite 9 long; gonopod 9 short, without nematiform setae on subapical setose organ. Spermatheca long and thin (fig. 164, sp), entering the apical region bursa copulatrix independently from median oviduct; helminthoid sclerite broad and short (fig. 165, hs); bursa copulatrix with accessory gland long and with the apical region expanded (fig. 164, acg), entering bursa copulatrix near spermatheca and without basal sclerite, bursa with sclerite on the base of oviduct.

Geographical Distribution: The two species of the genus *Oregus* occur in New Zealand, in the South Island.

Material Examined: *Oregus inaequalis* (AMNH, CUIC, MCZ) and *O. aereus* (AMNH, MCZ, USNM).

Percosoma Schaum, 1858

Figures 166–174

Percosoma Schaum, 1858: 356. Putzeys, 1868: 321; 1873: 316. Sloane, 1892: 58. Csiki, 1928: 20. Moore, 1960: 173. Lawrence et al., 1987: 121.

Type Species (by subsequent monotypy in Schaum, 1858): *Broscus carenoides* White, 1846.

Diagnosis: *Percosoma* is characterized, within Nothobroscina, by having setiferous punctures on vertex and pronotum with 12–18 setae on each side.

Description: External morphology (figs. 166–167): Head with one to four supraorbital punctures each side, each bearing a seta; and one to three setae at each side of vertex; without transverse impression in vertex and frontal impressions; temporal ridge distinct at the apical region; antenna with antennomeres 1 and 2 glabrous, 3–4 with apical ring, 5–11 setose throughout. Mandibles without scrobal setae. Maxillary eustipes with three basal setae. Labium with 6–16 setae on submentum; mentum ventral surface almost plane, with tooth bifid; prementum with glossal sclerite bisetose apically, ventral surface keeled longitudinally. Pronotum constricted apically (fig. 166), with 12–18 setae each side. Elytron with parascutellar striole joined to apical portion of stria 1; without parascutellar seta; with row of setiferous punctures in 5th elytral stria; lateral umbilical series with 18 setae. Foreleg trochanter bisetose; foretibia not prolonged externally; male fore and middle tarsomeres without adhesive vestiture.

Male genitalia (figs. 168–172): Sternum 9 with sclerotized ring complete with lateral margins wide. Median lobe with dorsal surface sclerotized on basal half (fig. 170); basal orifice completely closed dorsally with secondary membrane partially sclerotized (fig. 170) forming the basal keel. Internal sac with sclerite X broad, without lateroapical projections (figs. 171–172); apical plate of long spiculae and a bifid tooth. Left and right parameres setose on apical half (figs. 168–169).

Female genital tract (figs. 173–174): Rami of gonocoxite 9 long and thin. Subgonocoxite 9 broad, with three internal and one external ensiform setae; gonopod 9 short, without nematiform setae on subapical setose organ. Spermatheca thin, entering the apical region bursa copulatrix independently from median oviduct; helminthoid sclerite broad and long, with apical region separated from vaginal apophysis (fig. 174, hs); accessory gland long, without basal sclerite; bursa without sclerite on base of oviduct.

HABITAT: The genus inhabits wet forest (Darlington, 1961; Lawrence et al., 1987).

GEOGRAPHICAL DISTRIBUTION: The species of *Percosoma* occur in Tasmania and New Caledonia.

REMARKS: *Percosoma*, as presently considered, includes three species. The last revision of the genus was made by Sloane (1892), who established two main groups of species (Australian and Tasmanian). The Australian species are considered in the present revision as belonging to *Chylnus*, as explained above.

MATERIAL EXAMINED: *Percosoma carenoides* (AMNH, USNM); *Percosoma sulcipenne* (AMNH).

Mecodema Blanchard, 1853

Figures 175–188

Mecodema Blanchard, 1853: 34. Putzeys, 1868: 306; 1873: 307. Broun, 1880: 7; 1881: 653; 1866: 744. Csiki, 1928: 16. Hudson, 1934: 32. Britton, 1949: 543. Townsend, 1965: 302.

TYPE SPECIES (by monotypy): *Mecodema sculpturatum* Blanchard, 1853.

DIAGNOSIS: *Mecodema* belongs to a monophyletic group of Nothobroscina defined by a single supraorbital puncture each side of head, each bearing more than one seta. It differs from other genera of this group in having antennomeres 5–11 setose throughout.

DESCRIPTION: External morphology (figs. 175–177): Head with a single supraorbital puncture each side, each bearing more than one seta; vertex generally punctured; temporal ridge distinct at the apical region; antenna with antennomeres 1 and 2 glabrous, 3–4 with apical ring, 5–11 setose throughout. Mandibles without scrobal setae. Maxillary eustipes with two basal setae. Labium with four to six setae on submentum; mentum without rounded paramedian foveae; tooth of mentum bifid; prementum with glossal sclerite bisetose apically, ventral surface keeled longitudinally (fig. 177). Pronotum constricted apically, with 6 to 12 setae each side. Elytron with parascutellar striole joined to the apical portion of stria 1; without parascutellar seta; with row of setiferous punctures on 7th interval; lateral umbilical series with 15 setae. Foreleg trochanter with one seta; foretibia externally prolonged to the apex; male fore and middle tarsomeres without adhesive vestiture.

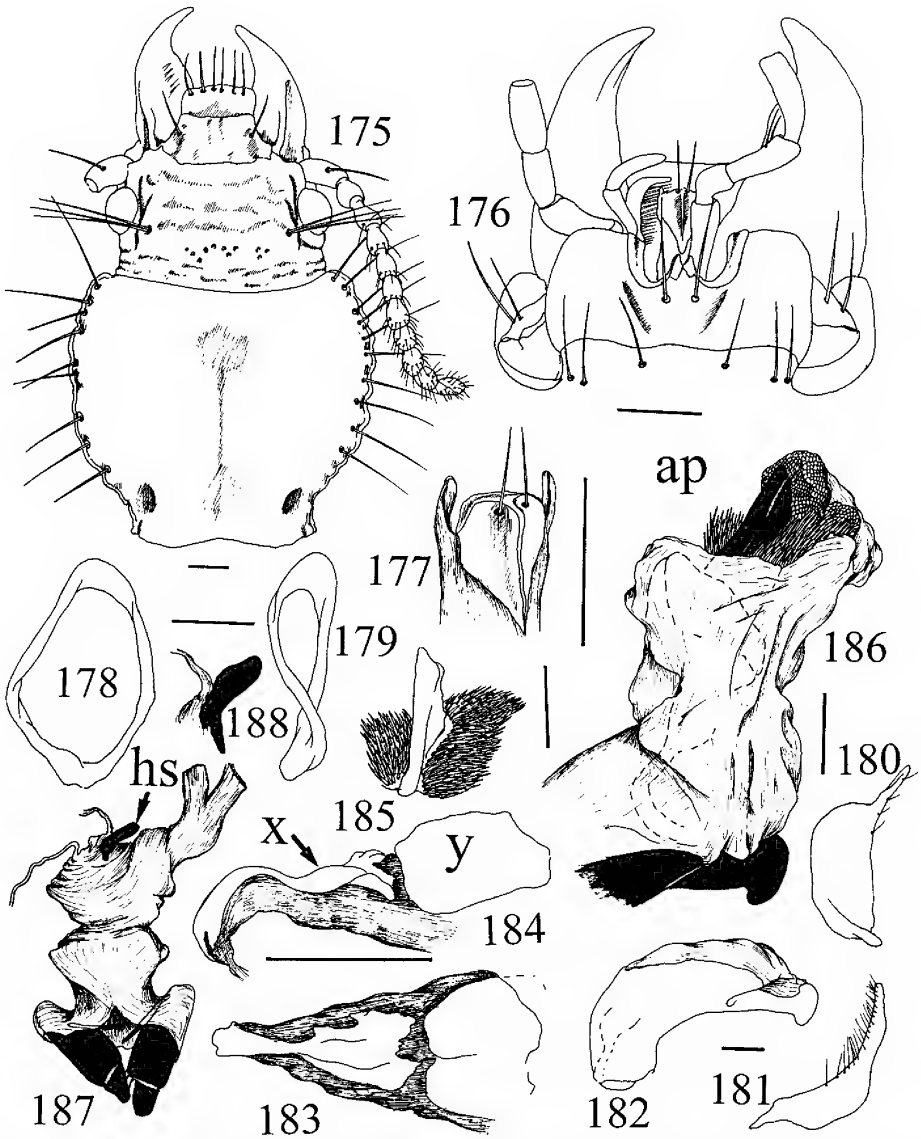
Male genitalia (figs. 178–186): Sternum 9 with sclerotized ring complete with lateral margins wide (figs. 178–179). Median lobe with dorsal surface sclerotized on basal third (fig. 182) and basal orifice completely closed dorsally (fig. 182), without basal keel. Internal sac with sclerite X elongated and curved, markedly expanded at the apical region as a plate; without lateroapical projections (figs. 183–184); apical plate of long spiculae and with a central tooth (figs. 185–186). Left paramere with few apical setae (fig. 180); right paramere with seta on apical half (fig. 181).

Female genital tract (figs. 187–188): Rami of gonocoxite 9 long and thin. Subgonocoxite 9 long, with an internal row of ensiform setae; gonopod 9 short, without nematiform setae on subapical setose organ. Spermatheca long and thin, entering the apical region bursa copulatrix independently from median oviduct; helminthoid sclerite broad and long, with the apical region separated from vaginal apophysis (fig. 188); accessory gland of bursa near spermatheca, without basal sclerite; bursa without sclerite on the base of oviduct.

HABITAT: The species are usually found in mountain and island habitats (Hudson, 1934). The distribution of some species seems to be associated with climatic factors, particularly with rainfall (e.g., *M. rugiceps* does not extend to areas receiving less than 1500 mm (60 in.) of annual rainfall). Some species occur above 920 m, and others from sea level to more than 1500 m, and they are found in the moist conditions of the dense forest or under stones on dry alpine screes. However, this latter habitat is often much damper than the former, as the loose stones provide against insolation from the sun (Townsend, 1965).

GEOGRAPHICAL DISTRIBUTION: The species of the genus *Mecodema* occur in New Zealand and Auckland Island.

REMARKS: *Mecodema* is one of the most diversified genera (like *Promecoderus*), with about 60 species. However, all the species examined share a synapomorphy: the enlarged apical region of sclerite X (fig. 186). *Mecodema* was studied by Britton (1949), who organized the 57 species into eight species groups. Townsend (1965) analyzed the



Figs. 175–188. *Mecodema crenicolle*. (**175**) Head and prothorax; (**176**) mouthparts, ventral view; (**177**) ligula, ventral view; (**178**) sternum 9, ventral view; (**179**), sternum 9, lateral view; (**180**) left paramere; (**181**) right paramere; (**182**) median lobe; (**183**) sclerite X, dorsal view; (**184**) sclerite X, lateral view; (**185**) apical plate; (**186**) internal sac showing the position of apical plate; (**187**) female genital tract, ventral view; (**188**) spermatheca and helminthoid sclerite. See appendix 2 for abbreviations.

species from South Island, describing new subspecies and species.

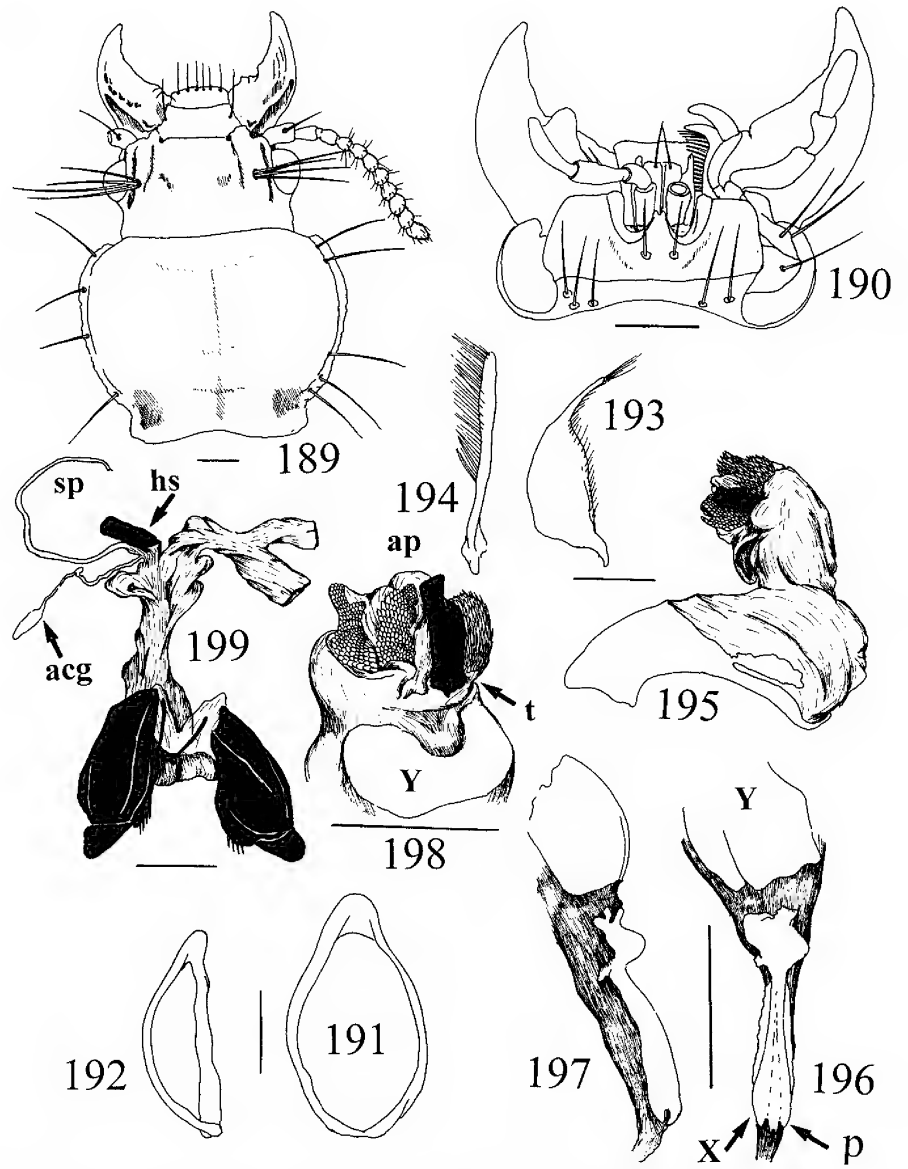
MATERIAL EXAMINED: *M. crenaticolle* (USNM); *M. crenicole* (USNM); *M. costellum* (CUIC); *M. howitti* (MCZ); *M. impressum* (MCZ); *M. oblongum* (USNM); *M. rectolineatum* (USNM); *Mecodema sculpturatum* (AMNH).

Metaglymma Bates, 1867

Figures 189–199

Metaglymma: Bates, 1867: 78. Putzeys, 1868: 318; 1873: 311. Broun, 1880: 10; 1886: 745, 818. Csiki, 1928: 18. Britton, 1949: 578.

Maoria Castelnau, 1867: 77 (type species *Maoria tibiale* Castelnau, by posterior designation in Britton, 1949). Castelnau, 1868: 163.



Figs. 189–199. *Metaglymma moniliforme*. (**189**) Head and prothorax; (**190**) mouthparts, ventral view. *Metaglymma tibialis*: (**191**) sternum 9, ventral view; (**192**) sternum 9, lateral view; (**193**) left paramere; (**194**) right paramere; (**195**) median lobe; (**196**) sclerite X, dorsal view; (**197**) sclerite X, lateral view; (**198**) apical plate. *Metaglymma moniliforme*: (**199**) female genital tract, ventral view. See appendix 2 for abbreviations.

TYPE SPECIES (by monotypy): *Metaglymma monilifer* Bates, 1867.

DIAGNOSIS: *Metaglymma* belongs to the same group as *Mecodema*, but differs from the latter in having antennomeres 3–11 with only an apical ring of setae.

DESCRIPTION: External morphology (figs. 189–190): Head with a single supraorbital puncture each side bearing more than one seta; temporal ridge distinct at apical region; antenna with antennomeres 1 and 2 glabrous, remaining only with an apical ring of setae. Mandibles without scrobal setae. Maxillary eustipes with two basal setae. Labium with

five to six setae on the submentum; mentum ventral surface without rounded paramedian foveae; tooth of mentum bifid; premetum glossal sclerite bisetose apically, ventral surface keeled longitudinally. Pronotum constricted apically, with five to six setae each side. Elytron with parascutellar striole joined to apical portion of stria 1; parascutellar setae absent; elytra with row of setiferous punctures on 7th interval; lateral umbilical series with 12–15 setae. Foreleg with trochanter with one seta; fore and middle tibiae elongate externally to the apex; male fore and middle tarsomeres without adhesive vestiture.

Male genitalia (figs. 191–198): Sternum 9 with sclerotized ring complete and lateral margins wide (figs. 191–192). Median lobe with dorsal surface sclerotized on basal third (fig. 195) and basal orifice completely closed dorsally, without basal keel. Internal sac with sclerite X broad and expanded near insertion of ejaculatory duct at its basal extremity (figs. 196–197); without lateroapical projections; apical plate of short spiculae and a central tooth (fig. 198, t). Left paramere setose along inner side (fig. 193); right setose (fig. 194).

Female genital tract (fig. 199): Rami of gonocoxite 9 long and thin. Subgonocoxite 9 long, with internal row of ensiform setae; gonopod 9 short, without nematiform setae on subapical setose organ. Spermatheca long and thin (fig. 199, sp), entering the apical region bursa copulatrix independently from median oviduct; helminthoid sclerite broad and long, with apical region separated from the vaginal apophysis (fig. 199, hs); accessory gland of bursa near spermatheca (fig. 199, acg), without basal sclerite; bursa without sclerite on base of oviduct.

HABITAT: *Metaglymma* species inhabit inland areas.

GEOGRAPHICAL DISTRIBUTION: The three species of *Metaglymma* occur in New Zealand, in South Island.

MATERIAL EXAMINED: *Metaglymma monilifer* (USNM); *M. tibiale* (USNM); *M. aberrans* (USNM).

Brullea Castelnau, 1867

Figures 200–205

Brullea Castelnau, 1867: 79; 1868: 166. Putzeys, 1868: 318; 1873: 319. Broun, 1880: 14. Csiki, 1928: 23. Britton, 1949: 581.

TYPE SPECIES (by monotypy): *Brullea antarctica* Castelnau 1867.

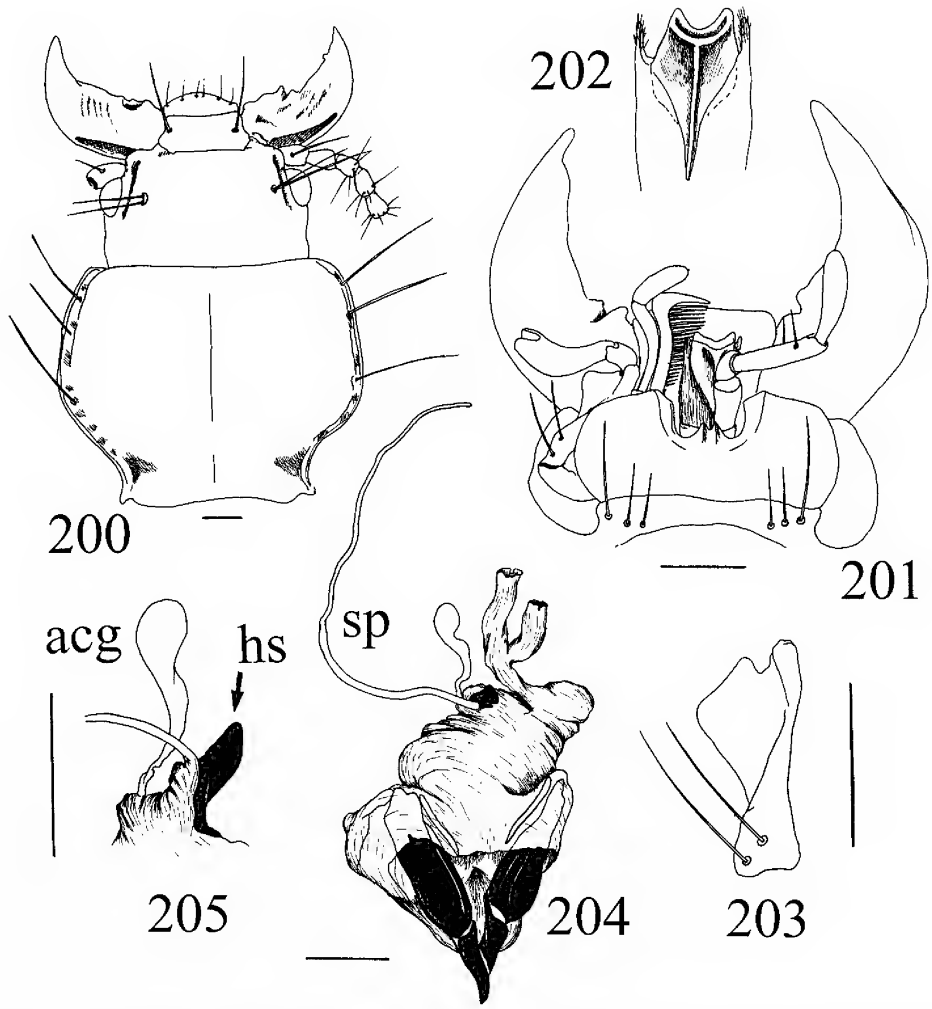
DIAGNOSIS: *Brullea* belongs to the same group as *Mecodema* and *Metaglymma*, and differs from those genera in having 3–4 setae on each side of pronotum.DESCRIPTION: External morphology (figs. 200–203): Head with single supraorbital puncture each side, bearing more than one seta; temporal ridge distinct at apical region; antenna with antennomere 1 and 2 glabrous, remaining only with an apical ring. Mandibles without scrobal setae. Maxillary stipes broad and expanded laterally, with two basal setae (fig. 203). Labium with six setae on the submentum; mentum ventral surface almost plane; tooth of mentum bifid; prementum with glossal sclerite asetose, ventral surface keeled longitudinally (fig. 202). Pronotum constricted apically, with 3–4 setae each side. Elytron with parascutellar striole joined to the apical portion of stria 1; parascutellar setae absent; elytra with eight setiferous punctures on 7th interval in row; lateral umbilical series with 10–11 setae. Foreleg trochanter with one seta; foretibia externally prolonged to a point at apex; middle and hind tibiae markedly curved and expanded at apex, markedly punctuated on outer side; male fore and middle tarsomeres without adhesive vestiture.

Male genitalia (After Ball, 1956 and Britton, 1949): Median lobe with dorsal surface sclerotized and basal orifice completely closed dorsally and without basal keel. Internal sac with sclerite X broad, without lateroapical projections. Left paramere setiferous.

Female genital tract (figs. 204–205): Rami of gonocoxite 9 long and thin. Subgonocoxite 9 long, without an internal row of ensiform setae; gonopod 9 long, without nematiform setae on subapical setose organ. Spermatheca long and thin (fig. 204, sp), entering apical region bursa copulatrix independently from median oviduct; helminthoid sclerite broad and long, with the apical region separated from vaginal apophysis (fig. 205, hs); accessory gland of bursa in apical region of bursa copulatrix, near spermatheca (fig. 205, acg), without basal sclerite; bursa without basal sclerite on the base of oviduct.

LARVAE: Only the final instar larva is known (Harris, 1978, 1980).

HABITAT: This species inhabits the coastal



Figs. 200–205. *Brullea antarctica*. (**200**) Head and prothorax; (**201**) mouthparts, ventral view; (**202**) ligula, ventral view; (**203**) eustipes, ventral view; (**204**) female genital tract, ventral view; (**205**) spermatheca and helminthoid sclerite. See appendix 2 for abbreviations.

psammophile habitats on sand dunes (Bull, 1948) or above high water marks (Hudson, 1934). It has special fossorial adaptations (Watt, 1975) and is confined to the supralittoral fringe of sandy beaches (Harris, 1978).

GEOGRAPHICAL DISTRIBUTION: The unique species of *Brullea* occurs in North and South Island of New Zealand.

MATERIAL EXAMINED: *Brullea antarctica* (USNM).

BARYPINA JEANNEL, 1941

TYPE GENUS: *Barypus* Dejean, 1828.

TAXA INCLUDED: Jeannel (1941) considered this group to include *Barypus* and the Australian and New Zealand genera of Broscini that have the basal orifice of median lobe completely closed. However, Ball (1956) included only *Barypus*. I considered this subtribe as Ball conceived it, to include only *Barypus* and a new genus described herein. The other genera considered by Jeannel are included in the subtribe Nothobroscina.

Barypina includes 23 species in two genera, *Barypus* and *Microbarypus* new genus (monospecific) both from southern South America. consider *Microbarypus* at generic rank, and not a subgenus of *Barypus* because

the two are largely different. *Barypus* shows several synapomorphies that traditionally define its species, and the inclusion of *Microbarypus* would imply a complete different and new redefinition of *Barypus*.

Barypina is the sister group of Creobiina. In both subtribes, the internal sac has lost the sclerites X and Y and the apical plate; also, the female genital tract has lost its vaginal apophysis. In terms of synapomorphies, Barypina is among the most distinctive groups in the entire tribe, as shown in figure 15. Besides sharing several features with Creobiina and allied genera, Barypina shows outstanding similarities to the *Oregus* clade in the structures of the mouthparts. The basal keel on the median lobe, a character used by Ball (1956) to define the subtribe Barypina, is present at different degrees in the genera *Oregus* (figs. 159–160) and *Percosoma* (fig. 170), indicating that this structure may have evolved independently.

The barypine species live in different habitats. The species of *Barypus* live in grassland or shrubby arid habitats, while *Microbarypus* inhabits the *Nothofagus* forest.

Key to genera of Barypina

1. Antennomeres 5–10 with a row of setae; 2–4 setae on submentum; male middle tarsomeres without adhesive vestiture ventrally; abdominal sterna 5–7 with complete basal groove; left paramere asetose . . . *Barypus*

1′. Antennomeres 5–10 without a row of setae; 6 setae on submentum; male with middle tarsomeres having adhesive vestiture ventrally; abdominal sterna 5–7 without groove; left paramere setose . . . . . *Microbarypus*

Barypus Dejean, 1828

Figures 206–218

Barypus Dejean, 1828: 24. Chaudoir, 1861: 526; 1876: 124. Putzeys, 1868: 306. Roig-Juñent. 1992a: 89; 1992b: 1.

Arathymus Guérin-Méneville, 1841: 188 (as subgenus of *Cnemacanthus*, type species: *Cnemacanthus parallelus* Guérin-Méneville, 1838 by original designation).

Odontomerus Solier, 1849: 240 (type species *Odontomerus subsulcatus* Solier, 1849 by monotypy) (= *Cnemacanthus parallelus* Guérin-Méneville).

Cardiophthalmus Curtis, 1839: 184 (type species *Cardiophthalmus clivinoides* Curtis, 1839 by monotypy).

Tetraodes Blanchard, 1853: 36 (type species *Tetraodes laevis* Blanchard 1853 by monotypy, = *Cardiophthalmus clivinoides* Curtis).

Type Species: (by original designation): *Molops rivalis* Germar, 1824.

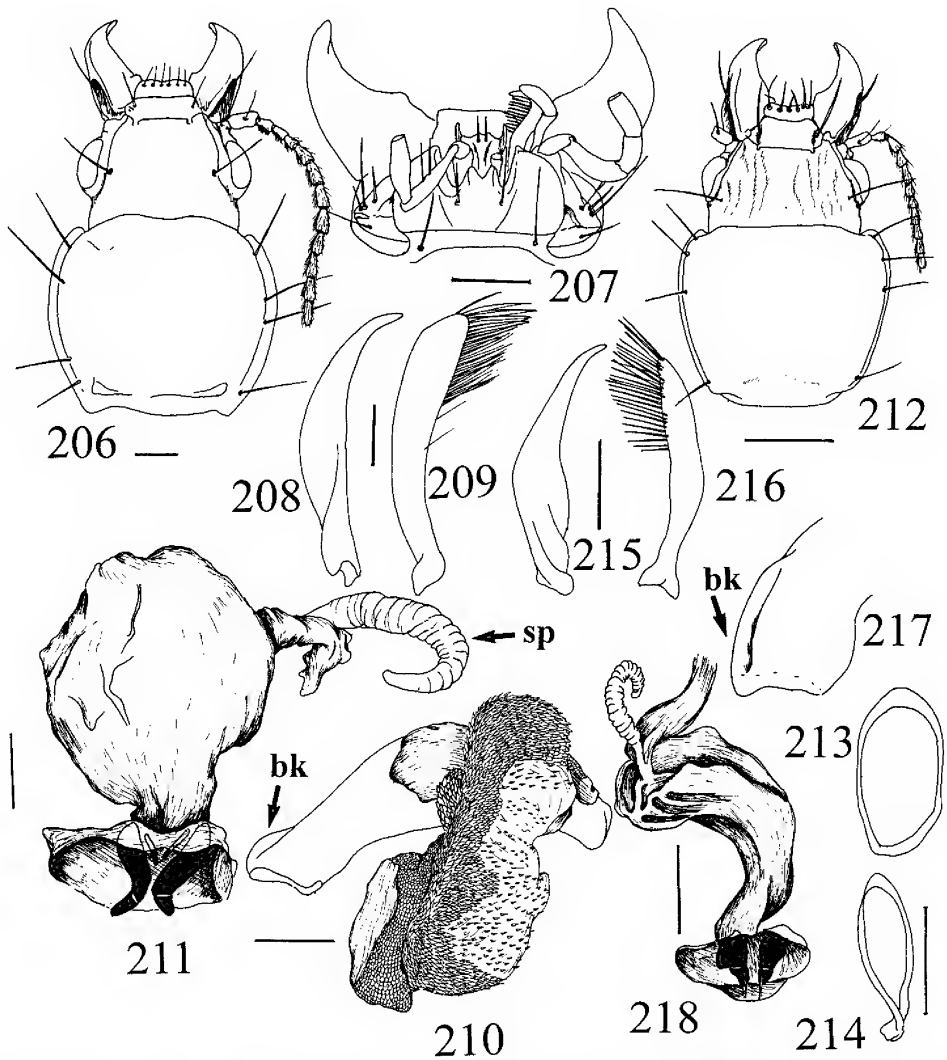
Diagnosis: *Barypus* is the only broscine genus that has a distinctly developed basal keel on median lobe.

Description: External morphology (figs. 206–207, 212): Head with a single supraorbital puncture on each side, each bearing one seta; without temporal ridge; eyes emarginates; antenna with antennomeres 2–3 with a group of setae in the lateroposterior side, 4 setose on apical half, remaining pubescent all along the surface. Mandibles each with scrobal setae. Maxillar eustipes with three basal setae. Labium with two to four setae on the submentum; tooth of mentum bifid; prementum with glossal sclerite bisetose apically, ventral surface markedly keeled longitudinally. Pronotum not constricted apically, with two to six setae each side; prosternum with apical setae. Elytron with parascutellar striole isolated from apical portion of stria 1; parascutellar setae absent; rows of setiferous punctures in the 1st, 3rd, 5th, and 7th intervals present or absent; lateral umbilical series with 6–51 setae. Abdominal sterna 5–7 with a transverse groove. Foreleg trochanter with one or two setae; foretarsomeres 1–2 with or without adhesive vestiture, middle tarsomeres without it.

Male genitalia (figs. 208–210, 213–217): Sternum 9 with sclerotized ring complete with lateral margins narrow (figs. 213–214). Median lobe with dorsal surface sclerotized on basal half (fig. 210) and basal orifice completely closed dorsally, with basal keel distinctly developed (fig. 210, 217, bk). Internal sac without sclerites X and Y and apical plate (fig. 210). Left paramere asetose (figs. 208, 215); right paramere setose (figs. 209, 216).

Female genital tract (figs. 211, 218): Rami of gonocoxite 9 long. Gonopod 9 varies in size, with or without nematiform setae on subapical setose organ. Spermatheca short and broad (fig. 211, sp), joined in a common duct before entering the bursa copulatrix with median oviduct (fig. 218); helminthoid sclerite absent; bursa copulatrix and spermatheca without accessory glands.

Habitat: This genus occurs in grassland



Figs. 206–218. *Barypus*. **(206–211)** *Barypus (Barypus) clivinoides*: (**206**) head and prothorax; (**207**) mouthparts, ventral view; (**208**) left paramere; (**209**) right paramere; (**210**) median lobe; (**211**) female genital tract, ventral view. **(212–218)** *Barypus* (*Arathymus*) *bonvouloiri*: (**212**) head and prothorax; (**213**) sternum 9, ventral view; (**214**) sternum 9, lateral view; (**215**) left paramere; (**216**) right paramere; (**217**) base of median lobe showing basal keel; (**218**) female genital tract, lateral view. See appendix 2 for abbreviations.

areas of southern South America. The species inhabit Patagonian steppes, pampas of Uruguay and Argentina, grasslands of the Sierras of Córdoba, San Luis, and Salta provinces, in Argentina, and the bushy central regions of Chile.

GEOGRAPHICAL DISTRIBUTION: *Barypus* extends south of latitude 25° in Argentina, Uruguay, and central Chile.

MATERIAL EXAMINED: *Barypus* (*A.*) *bonvouloiri* (MLPA); *B.* (*A.*) *parallelus* (CIUC, MCZ); *B.* (*B.*) *comechingonensis* (CM, IADIZA, MLPA); *B.* (*B.*) *pulchellus* (CUIC, MLPA); *B.* (*B.*) *rivalis* (CUIC, MLPA); *B.* (*C.*) *clivinoides* (CUIC, IADIZA, MCZ, MLPA), *B.* (*C.*) *chubutensis* (IADIZA); *B.* (*C.*) *longitarsis* (IADIZA, MLPA); and *B.* (*C.*) *mendozensis* (IADIZA).

REMARKS: The systematics of the 22 species of *Barypus* has been recently elucidated

by Roig-Juñent and Cicchino (1989) and Roig-Juñent (1992a, 1992b) who recognize the three subgenera proposed by Putzeys (1868) and conducted a cladistic analysis of their species (Roig-Juñent, 1995b).

KEY TO SUBGENERA OF *BARYPUS*

1. Dorsal surface with metallic coloration; four setae on submentum; front with two longitudinal grooves ... *Barypus* (*Barypus*)
- Dorsal surface without metallic coloration; two setae on submentum; front without longitudinal grooves 2
2(1). Antennomeres moniliform; six setae in lateral umbilical series; foretrochanter with two setae ..... *Barypus* (*Arathymus*)
- Antennomeres filiform; 24–51 setae in lateral umbilical series; foretrochanter with one setae... *Barypus* (*Cardiophthalmus*)

Microbarypus, new genus

Figures 219–227

TYPE SPECIES: *Microbarypus silvicola* new species.

ETYMOLOGY: The generic name refers to its small size, compare to species of related genus *Barypus*.

DIAGNOSIS: *Microbarypus* and *Barypus* are the only broscine genera with eyes emarginate in front of the antennal insertion. *Microbarypus* differs from *Barypus* in having antennomeres without a row of setae, prosternum with setae, male middle tarsomeres with adhesive vestiture ventrally, abdominal sterna 5–7 without a transverse groove, and basal keel of median lobe small.

DESCRIPTION: External morphology (figs. 219–220): Head with one single supraorbital puncture each side, bearing one seta; front with a shallow longitudinal sulcus or without it; without temporal ridge; eyes with emargination; antenna with antennomere 2 with an apical ring of setae, the remaining pubescent all along the surface. Mandibles each with scrobal setae. Maxillary eustipes with three basal setae. Labium with six setae on submentum; tooth of mentum bifid; prementum with glossal sclerite bisetose apically, ventral surface keeled longitudinally. Pronotum not compressed apically, with two setae each side; prosternum with apical setae. Elytron with parascutellar striole isolated from apical portion of stria 1; without parascutellar seta; without setiferous punctures in the 1st, 3rd, 5th, and 7th intervals; lateral umbilical series with 12–17 setae. Abdominal sterna 5–7 smooth. Foreleg trochanter with one or two setae; male foretarsomeres 1–2 and middle tarsomeres 1–2 with adhesive vestiture ventrally.

Male genitalia (figs. 221–226): Sternum 9 with sclerotized ring complete with lateral margins narrow (figs. 221, 222). Median lobe with dorsal surface almost completely sclerotized (figs. 225, 226) and basal orifice completely closed dorsally; with basal keel distinctly developed (figs. 225, 226, bk). Internal sac without sclerites X, Y, and apical plate. Left and right parameres setiferous (figs. 223, 224).

Female genital tract (fig. 227): Rami of gonocoxite 9 long. Gonopod 9 long, with nematiform setae on subapical setose organ. Spermatheca broad, joined in a common duct before entering bursa copulatrix with median oviduct; helminthoid sclerite absent; bursa copulatrix and spermatheca without accessory glands. Bursa copulatrix without sclerites.

GEOGRAPHICAL DISTRIBUTION: *Microbarypus* occurs in the *Nothofagus* forest of Chiloé Continental, in Chile.

REMARKS: This new genus is very interesting because it links *Barypus* with Creobiina. *Barypus* was problematic because of its numerous autapomorphic states, both from external morphology and genitalic features. *Microbarypus* has apomorphic external morphological features only shared (as synapomorphies) with *Barypus*, but several of its genital features are characteristic of creobiines, especially the female genital tract.

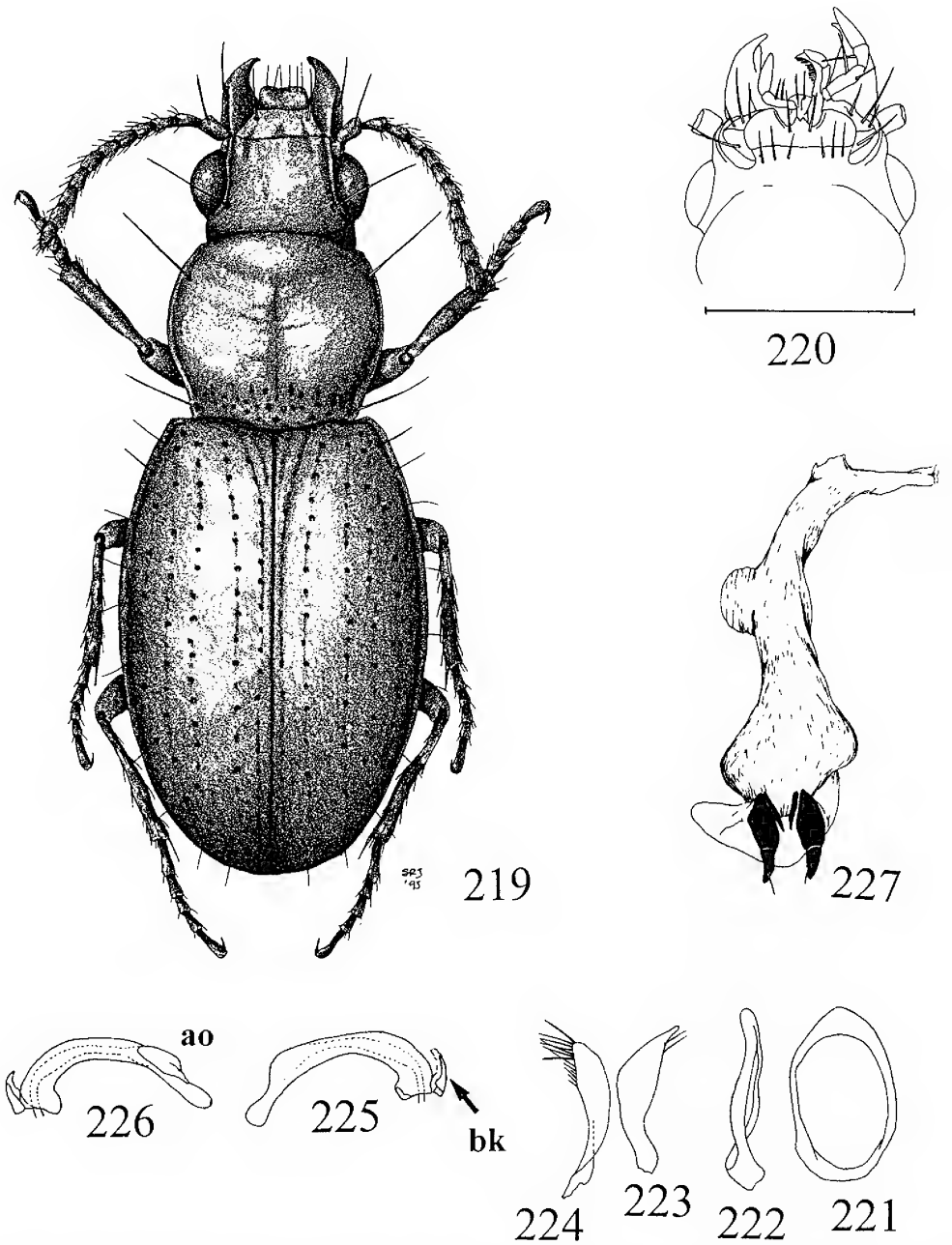
Microbarypus silvicola, new species

HOLOTYPE: Male, Chile, Aisén, Alto Queulat (Paso), 8-XII-1986, col. S. Roig (IADIZA).

ALLOTYPE: Female, Chile, Puerto Bella Vista, Seno Ultima Esperanza, col F. Roig (IADIZA).

ETYMOLOGY: A Latin adjective, the specific epithet refers to the species habitat, a cool rainforest of *Nothofagus* species.

DIAGNOSIS: Adults of this species are readily distinguished from other South American broscines by its small size.



Figs. 219–227. *Microbarypus sylvatica*. (**219**) Habitus, dorsal view; (**220**), mouthparts, ventral view; (**221**) sternum 9, ventral view; (**222**) lateral view; (**223**), left paramere; (**224**) right paramere; (**225**) median lobe, lateral view; (**226**) lateral view; (**227**) female genital tract, ventral view. See appendix 2 for abbreviations.

DESCRIPTION: The following features are added to the generic characters: Habitus as in figure 219. Small size (for Broscini): length 11.86–13.06 mm. Body color of dorsal surface from dark reddish to black; antennae, mouthparts, and legs almost dark reddish (one specimen is black).

Head: Frontal impressions linear, posteri-

orly divergent; vertex with shallow transverse impression, indistinct medially; postocular prominences distinct each side. Eyes rounded, prominent.

Thorax: Pronotum (fig. 219) with disc slightly convex, almost as long as broad, apical margin truncate, basal margin slightly sinuate; apex much wider than base; anterior angles rounded; sides convergent posteriorly; lateral margin with narrow bead, sinuate; posteriorly a shallow basolateral fovea each side; single marginal setiferous puncture each side, near middle. Anterior margin of prosternum emarginate.

Elytra convex, oval, with steep apical declivity, striate, with flat intervals.

Legs: Foretrochanter bisetose; forefemur markedly swollen in middle of ventral margin.

Abdomen: Sterna 4–7 smooth, each with a pair of paramedian setae.

Male genitalia: Besides the generic characteristics: median lobe curved, thin (figs. 225, 226), with broad apex; apical orifice small, central.

Female genital tract (fig. 227): Bursa copulatrix long with a central expansion.

HABITAT: The *Nothofagus* forest. Specimens collected are reported from the *Nothofagus dombeyi* forest of Chiloé Continental.

DISTRIBUTION: The species is known only in Chile.

CREOBIINA JEANNEL, 1941

Cnemacanthini Lacordaire, 1854: (*Cnemacanthus* Gray, 1832 = *Promecoderus* Dejean, 1829, non *Cnemacanthus* sensu Brullé, 1834).

Creobitae Jeannel, 1941: 287 (as a subfamily).

Creobiina: Ball, 1956: 45. Townsend, 1971: 180. Roig-Juñent, 1995a: 52.

TYPE GENUS: *Creobius* Guérin-Méneville, 1838.

REMARKS: The suprageneric name Cnemacanthini has strict priority over the name Creobiina. Nevertheless, use of Cnemacanthini would create confusion, since it was used as the tribal name for the genus *Cnemalobus*, a harpaline group (Roig-Juñent, 1993).

TAXA INCLUDED: The subtribe Creobiina remains as defined by Ball (1956) (table 3). It represents the largest group of Broscini in number of species (appendix 1). Jeannel (1941) considered Creobiina to include the austral genera with the basal orifice of median lobe open, and the genera *Miscodera* and *Broscodera*. Ball (1956) excluded these two genera from Creobiina, including them in Broscina. This is the viewpoint followed in this study.

The subtribe Creobiina comprises 11 genera with 97 species (only two genera are monospecific) (appendix 1).

Creobiina shares with the sister subtribe Barypina losses of sclerites affecting the male genitalia (without internal sclerites) and the female tract (spermatheca without vaginal apophysis). Creobiina shows nine synapomorphies, with only one unique derived feature: enlarged left paramere (53^2). The other structures suffer reversions within Creobiina or changes to another character state: the shape of mentum tooth (10^2); male foretarsomeres 1–4 with adhesive vestiture ventrally (44^1); rami of gonocoxite 9 absent (63^0). Several features are reversions to the plesiotropic condition: paraglossas short (16^1), median lobe with basal orifice completely open (54^0), dorsal surface membranous (55^0), and with basal expansions (56^1), or parallelism with other groups, like nematiform setae of subapical setose organ absent (64^1).

Within this subtribe, there are two clear monophyletic groups, also recognized by Ball (1956). One group includes four Australian genera, and is characterized by nine synapomorphies, five of them unique structures within the tribe: mentum without tooth (10^0), mesoepimera with carina (29^1), antecoxal suture of metasternum not visible (32^1), presence of a large tooth in the internal sac, that is seen in the apical orifice when the internal sac is not everted (62^1), and accessory gland in the spermatheca (70^1). Some genera of this group have large species, and some species have adaptations associated with fossorial habits, like fore and middle tibiae with lateral expansions, characters also present in *Brullea* (Nothobroscina).

The other group is a large clade, including the genus *Promecoderus* with 41 species. This clade is supported by three synapomorphies: glossal sclerite without carina (14^0), antennal pubescence from half of the third

antennomere (22^0), and presence of four setae on the glossal sclerite (15^2) as exclusive character within Broscini. The cladograms (figs. 14, 15) show that the relationships among the different genera are not resolved. Results of this study (fig. 15) show that the genus *Promecoderus* is not monophyletic and the taxonomic revision of this genus is necessary in order to clear up the different groups of species within it.

The two main groups of creobiines inhabit different habitats: one group, *Cerotalis* and related genera, are big to medium-size species and occur principally in dry habitats. The second group, *Promecoderus*, *Creobius*, *Cascellius*, and related genera, are small to medium-size, bright-green or brown species, and occur in *Nothofagus* forests.

Key to genera of Creobiina

1. Mentum without tooth, glossal sclerite bisetose apically, markedly keeled ventrally 2
- Mentum with tooth (variously developed), glossal sclerite quadrisetose apically, not keeled, at least with the paramedian areas deep-set 5

2(1). Fore and middle tibiae markedly palmate externally; foretibia with two middle external teeth ..... *Gnathoxys*
- Fore and middle tibiae not markedly palmate externally, and without middle teeth 3

3(2). Prosternum markedly projected backward posterior to the coxae.. *Brithysternum*
- Prosternum not distinctly projected backward posterior to the coxae 4

4(3). Labial palpomere 2 with four to eight setae; maxillary palpomeres 2 and 3 with one seta each; male middle tarsomeres without adhesive vestiture ... *Adotela*
- Labial palpomere 2 bisetose; maxillary palpomeres 2 and 3 without setae; male middle tarsomeres 1–2 or 1–3 with adhesive vestiture ..... *Cerotalis*

5(1). Head with three or more supraorbital setae over each eye, five setae on each lateral margin of pronotum .... *Creobius*
- One supraorbital seta over each eye; two or three setae on each lateral margin of pronotum 6

6(5). Elytron with 9–12 setae in lateral umbilical series; abdominal sterna smooth.. ..... *Bountya*
- Elytron with four setae in lateral umbilical series; abdominal sterna with or without lateral sulcus or fovea 7

7(6). Labial submentum bisetose 8
- Labial submentum with four or six setae 9

8(7). Eyes flat; tooth of labial mentum long; temporal ridge obsolete; apex of elytra curved; elytron with eight striae; males without adhesive vestiture on middle tarsomeres ..... *Nothocascellius*
- Eyes convex; tooth of labial mentum short; temporal ridge complete; apex of elytra not curved; elytral striae, between 6th and 7th with two or more supernumerary striae; males with adhesive vestiture on middle tarsomeres ..... *Cascellius*

9(7). Deep sulcus behind eyes, abdominal sterna 5–8 each with lateral sulcus (fig. 318) or lateral fovea at each side from with a transverse extended mediad ... ..*Promecoderus* (groups *brunnicornis* and *subdepressus-inornatus-gibbossus*)
- Sulcus behind eyes absent; abdominal sterna smooth or with lateral fovea (fig. 317), but without transverse line . . .10

10(9). Middle tarsomeres of male with adhesive vestiture ..... *Promecoderus*
- Males without adhesive vestiture on middle tarsomeres 11

11(10). Abdominal sterna smooth; male foretarsomeres with adhesive vestiture ....*Acallistus*
- Abdominal sterna 4-7 with two lateral foveae; male foretarsomeres without adhesive vestiture ..... *Anheterus*

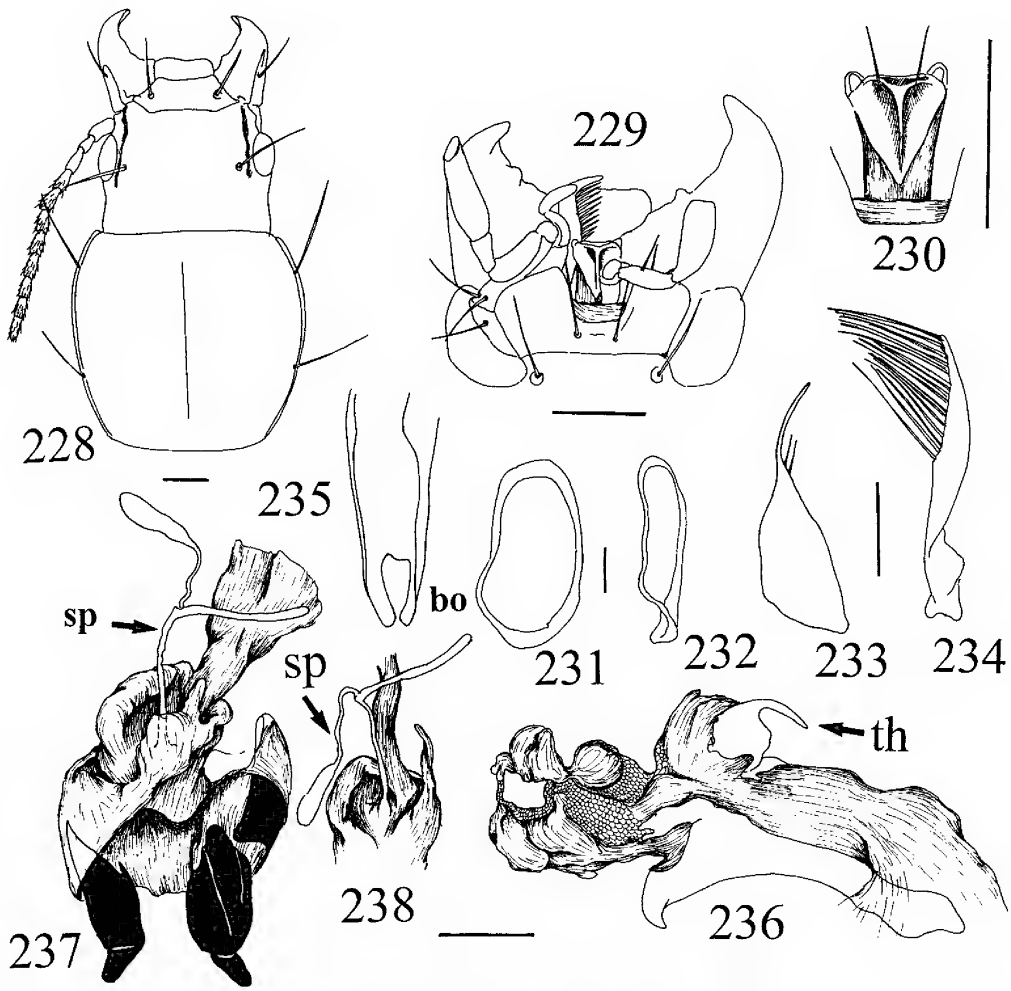
Cerotalis Castelnau, 1867

Figures 228–238

Cerotalis Castelnau, 1867: 89. MacLeay, 1873: 330. Sloane, 1890: 229. Csiki, 1928: 23. Lawrence et al., 1987: 118.

Promecoderus (part): Putzeys, 1868: 343; 1873: 337.

Type Species: *Cerotalis substriata* Castelnau 1867 (present designation). Three species were included by Castelnau (1867) in the description of the genus: *Cerotalis semiviolacea*, *C. substriata*, and *C. versicolor*. Subsequently Putzeys (1868) made a fine description of *C. substriata*, and referred the other two species described by Castelnau to *C. substriata*. For this reason, and because *C. substriata* has a wide distribution, I choose it as the type species.



Figs. 228–238. *Cerotalis substriata*. (**228**) Head and prothorax; (**229**) mouthparts, ventral view; (**230**) ligula, ventral view; (**231**) sternum 9, ventral view; (**232**) lateral view; (**233**) left paramere; (**234**) right paramere; (**235**) base of median lobe, dorsal view; (**236**) median lobe, lateral view, showing internal sac; (**237**) female genital tract, ventral view; (**238**) union of spermatheca and oviduct in bursa copulatrix. See appendix 2 for abbreviations.

DIAGNOSIS: *Cerotalis* belongs to a natural group of Broscini with several exclusive characters, like mentum without tooth and spermatheca with accessory gland. It differs from the other genera of this group in having male middle tarsomeres with adhesive vestiture ventrally.

DESCRIPTION: External morphology (figs. 228–230): Head with a single supraorbital puncture each side bearing one seta; vertex without a posterior transverse groove; temporal ridge complete; antenna with antennomeres 1 and 2 glabrous, 3 with apical ring; 4th setose on apical half, remaining pubescent all along the surface. Mandibles each with scrobal setae. Maxillary eustipes with two basal setae. Labium with two to four setae on submentum; tooth of mentum absent; prementum with glossal sclerite bisetose apically, ventral surface markedly keeled longitudinally (fig. 230). Pronotum not constricted apically, with two or three setae each side. Elytron with parascutellar striole joined to the apical portion of stria 1; with parascutellar setae on basal portion of second stria; lateral umbilical series with seven or

eight setae. Foreleg trochanter with one seta; foretibia expanded at apex; male foretarsomeres 1–4 and middle tarsomeres 1–2 or 1–3 with adhesive vestiture ventrally.

Male genitalia (figs. 231–236): Sternum 9 with a complete ring, with a portion not sclerotized, and lateral margins narrow (figs. 231–232). Median lobe with dorsal surface unsclerotized (fig. 235–236) and basal orifice completely open dorsally (fig. 235, bo); apical orifice open to the left. Internal sac without sclerite X, Y, and apical plate; armature consisting of groups of small spiculae and a sclerotized tooth near apical orifice (fig. 236, th). Left paramere with two apical setae (fig. 233); right setose on apical half (fig. 234).

Female genital tract (figs. 237–238): Rami of gonocoxite 9 absent. Subgonocoxite 9 long; gonopod 9 short, without nematiform setae on subapical setose organ. Spermatheca thin and long (figs. 237–238, sp), with accessory gland (fig. 237); without helminthoid sclerite; median oviduct and spermatheca enter separately into bursa copulatrix (fig. 238); bursa copulatrix short, without accessory gland; ligula unsclerotized.

HABITAT: Two species of *Cerotalis* occur in the Malle and Eremean zones (Matthews, 1980) in South Australia. They inhabit low open woodland (Lawrence et al., 1987).

GEOGRAPHICAL DISTRIBUTION: The seven species of the genus *Cerotalis* occur in Australia, in the west (Western Australia), south (South Australia and Victoria), and northwest (Queensland).

MATERIAL EXAMINED: *Cerotalis substriata* (AMNH, USNM).

Adotela Castelnau, 1867

Figures 239–249

Adotela Castelnau, 1867: 88. Putzeys, 1868: 347. MacLeay, 1873: 330. Putzeys, 1873: 337. Sloane, 1890: 229. Lawrence et al., 1987: 116.

Parroa Castelnau, 1867: 87. Putzeys, 1868: 349. MacLeay, 1873: 330. Csiki, 1928: 22. Lawrence et al., 1987: 116. No type species designated; species available from the original description: *Parroa carbonaria*, *P. bicolor*, *P. grandis*, *P. howittii*, and *P. violacea.* I could not find any reason to choose any of these species as the type. A systematic revision of the genus *Adotela* is needed. Then a basis for choosing the type species of *Parroa* could be established.

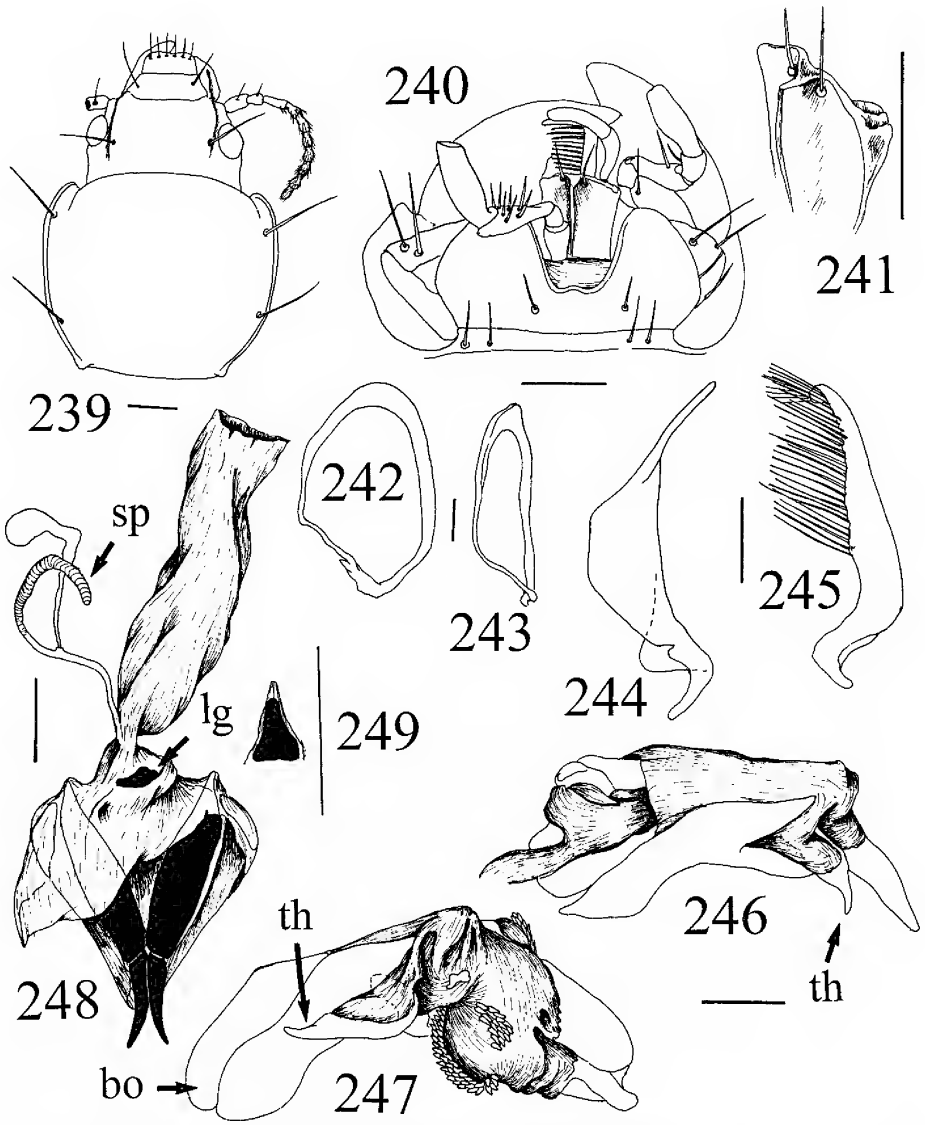
TYPE SPECIES: *Adotela concolor* Castelnau, 1867. PRESENT DESIGNATION. Two species of *Adotela* were included when Castelnau (1867) described the genus: *A. concolor* and *A. esmeralda.* Both species are only known from type locality (Lawrence et al., 1987). The original description of *A. esmeralda* is very poor (noted also by Sloane, 1890: 234), and therefore I choose *A. concolor* as type species, since it has a more complete original description.

DIAGNOSIS: *Adotela* belongs to the same group as does *Cerotalis*; differing from other genera of this group in having two setae on mentum and male middle tarsomeres without adhesive vestiture.

DESCRIPTION: External morphology (figs. 239–241): One supraorbital puncture bearing one seta on each side of head; vertex without posterior transverse groove; temporal ridge complete. Antenna with antennomeres 1 and 2 glabrous, 3–4 setose on apical region, 5–11 pubescent all along the surface. Mandibles each with scrobal setae present. Maxillary eustipes with two basal setae; maxillary palpomere 2 (and 3 in some species) with seta. Labium with two to four setae on submentum; tooth of mentum absent; mentum bisetose; prementum with glossal sclerite bisetose apically, ventral surface markedly keeled longitudinally (fig. 241); labial palpomere 2 with four to eight setae. Pronotum not constricted apically, with two setae each side. Elytron with parascutellar striole joined to the apical portion of stria 1; with parascutellar seta on basal portion of second stria; lateral umbilical series with 8 to 12 setae. Foreleg trochanter with one seta; foretibia expanded at apex; male foretarsomeres 1–3 with adhesive vestiture ventrally, middle tarsomeres without.

Male genitalia (figs. 242–247): Sternum 9 with complete sclerotized ring with lateral margins narrow (figs. 242–243). Median lobe with dorsal surface unsclerotized (fig. 246) and basal orifice completely open dorsally (fig. 247, bo). Internal sac without sclerite X, Y, and apical plate; armature consisting of groups of small spiculae and a sclerotized tooth near apical orifice (figs. 246–247, th). Left paramere asetose (fig. 244); right setose on apical half (fig. 245).

Female genital tract (figs. 248, 249): Rami



Figs. 239–249. *Adotela howitti*. (**239**) Head and prothorax; (**240**) mouthparts, ventral view; (**241**) ligula, lateral view; (**242**) sternum 9, ventral view; (**243**) lateral view; (**244**) left paramere; (**245**) right paramere; (**246**) median lobe, lateral view; (**247**) lateral view, showing internal sac; (**248**) female genital tract, ventral view; (**249**) ligula of bursa copulatrix. See appendix 2 for abbreviations.

of gonocoxite 9 absent. Subgonocoxite 9 long, thin, with ensiform setae; gonopod 9 long and sharp, without nematiform setae on subapical setose organ. Spermatheca thin and long (fig. 248, sp), with accessory gland; Helminthoid sclerite absent; median oviduct and spermatheca enter closely but separately into bursa copulatrix; bursa copulatrix short, without accessory gland; ligula sclerotized (fig. 249).

HABITAT: *A. apicalis* occurs in the Eremean zone (Matthews, 1980) in south Australia, inhabiting open scrub (Lawrence et al., 1987).

GEOGRAPHICAL DISTRIBUTION: The 17 species of the genus *Adotela* are widely distributed in Australia (New South Wales, Northern Territory, Queensland, Victoria, and Western Australia).

MATERIAL EXAMINED: *Adotela apicalis*

(MCZ); *A. bicolor* (MCZ); *A. esmeralda* (MCZ); *A. howitti* (CUIC, USNM); *A. noctis* (MCZ); *A.* aff. *noctis* (ANIC).

NOTES ABOUT SYNONYMY: Castelnau (1867) considered a separate genus for each sex, *Adotela* for the male and *Parroa* for the female. Putzeys (1873) and Sloane (1890) recognized that both forms were merely the different sexes of the same genus, and adopted the name *Adotela*, but did not designate a type species. Both authors used the name *Adotela* because this genus was correctly described by Castelnau (1867), while the description of *Parroa* was erroneous for some characters.

Gnathoxys Westwood, 1839

Figures 250–262

Gnathoxys Westwood, 1839: 89. Putzeys, 1868; 371; 1873: 342. Sloane, 1890: 190; 1910: 380. Csiki, 1928: 21. Lawrence et al., 1987: 118.

TYPE SPECIES: *Gnathoxys granularis* Westwood, 1839. PRESENT DESIGNATION. Two species of *Gnathoxys* were included when Westwood (1839) described the genus: *G. granularis* and *G. irregularis*. The original description of *G. irregularis* is very poor. For this reason and because *G. irregularis* is only known from type locality, I choose *G. granularis* as type species because it has a more complete original description.

DIAGNOSIS: *Gnathoxys* is the only broscine genera with foretibia having two medial teeth.

DESCRIPTION: External morphology (figs. 250–253): One supraorbital puncture bearing one seta on each side of head; vertex without posterior transverse groove; temporal ridge complete. Antenna with antennomeres 1–3 glabrous, 4 with apical ring of setae; 5–11 with pubescence all along the surface. Mandibles each with scrobal setae. Maxillary eustipes with three basal setae, maxillary palpomere 2 (and 3 in some species) with seta. Labium with submentum bisetose; mentum asetose; tooth of mentum absent; prementum with glossal sclerite bisetose apically, ventral surface markedly keeled longitudinally (fig. 252); labial palpomere 2 with one seta, last labial palpomer of male axiform (fig. 251). Pronotum not constricted apically, with two setae each side; prosternum with or without two apical dents. Elytron with parascutellar striole joined to apical portion of stria 1; with parascutellar setae on basal portion of second stria; lateral umbilical series with six to nine setae. Foreleg trochanter with one seta; foretibia prolonged externally to a point at the apex, with two medial teeth (fig. 253); and with a row of dorsal setae; male fore and middle tarsomeres without adhesive vestiture, asymmetric.

Male genitalia (figs. 254–259): Sternum 9 with a complete ring, a portion not sclerotized, and lateral margins narrow (figs. 254–255). Median lobe with dorsal surface completely membranous, unsclerotized (fig. 258); basal orifice completely open dorsally. Internal sac without sclerites X, Y, and apical plate, but with long sclerite from right side of apical orifice to end of internal sac (fig. 259, s); without sclerotized tooth near apical orifice. Left paramere asetose (fig. 256); right paramere setose on apical half (fig. 257).

Female genital tract (figs. 260–262): Rami of gonocoxite 9 absent. Subgonocoxite 9 long; gonopod 9 long and sharp, without nematiform setae on subapical setose organ. Spermatheca short, with (*G. tesselatus*, fig. 262) or without accessory gland (*G. granularis*, figs. 260–261); median oviduct and spermatheca enter separately into bursa copulatrix; helminthoid sclerite absent. Bursa copulatrix short, without accessory gland; ligula sclerotized (fig. 260, lg).

HABITAT: Two species of *Gnathoxys* occur on the Malle and dry sclerophill zone (Matthews, 1980), in South Australia, and all species have fossorial habits (Lawrence et al., 1987).

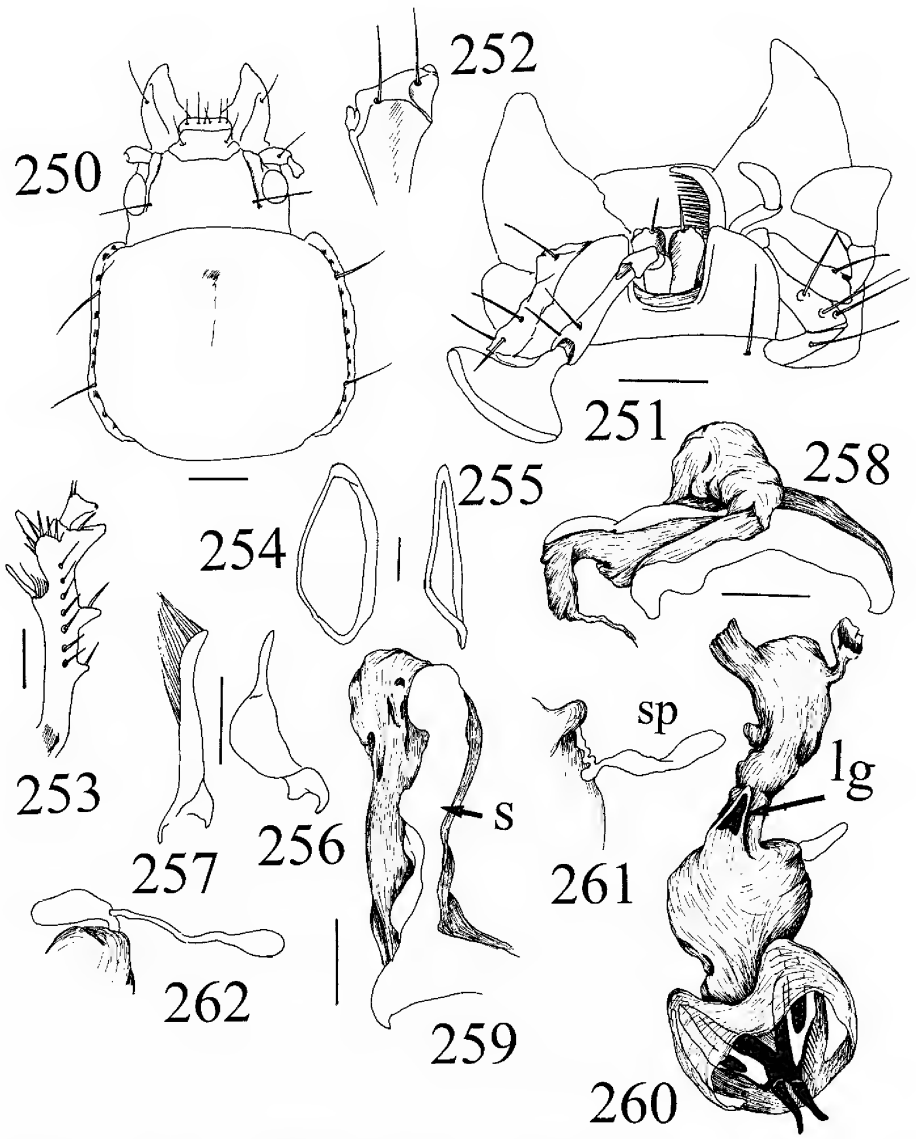
GEOGRAPHICAL DISTRIBUTION: The 16 species of the genus *Gnathoxys* are widely distributed in Australia (New South Wales, Northern Territory, Queensland, South Australia, Victoria, and Western Australia).

MATERIAL EXAMINED: *Gnathoxys cicatricosus* (MCZ); *G. granularis* (AMNH); *G. tesselatus* (MCZ).

Brithysternum MacLeay, 1873

Figures 263–274

Brithysternum MacLeay, 1873: 366. Sloane, 1910: 386. Csiki, 1928: 21. Lawrence et al., 1987: 115.

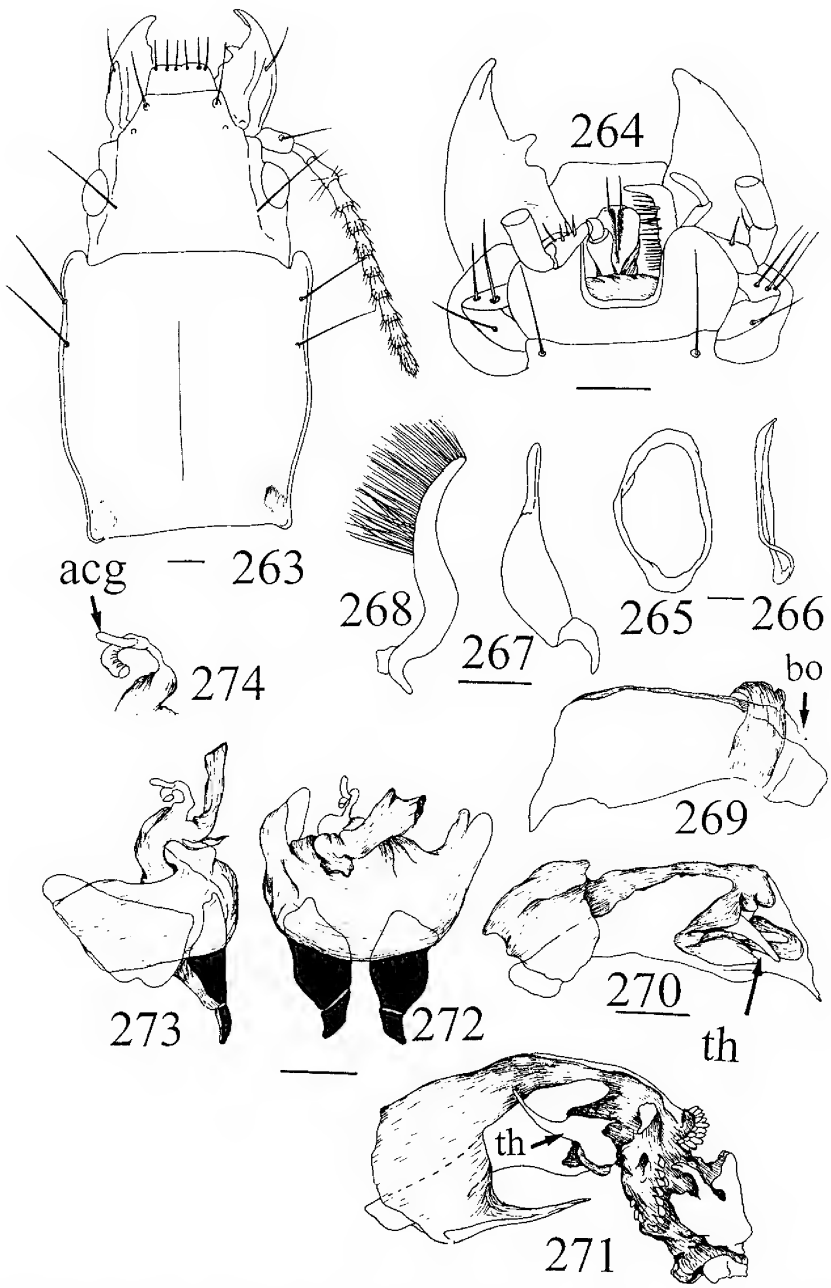


Figs. 250–262. *Gnathoxys*. (**250–261**) *Gnathoxys granularis*: (**250**) head and prothorax; (**251**) mouthparts, ventral view; (**252**) ligula, lateral view; (**253**) foretibia; (**254**) sternum 9, ventral view; (**255**) lateral view; (**256**) left paramere; (**257**) right paramere; (**258**) median lobe, lateral view; (**259**) lateral view, showing internal sac; (**260**) female genital tract, ventral view; (**261**) spermatheca. **(262)** *Gnathoxys tesselatus*: spermatheca with accessory gland. See appendix 2 for abbreviations.

TYPE SPECIES (by monotypy): *Brithysternum calcaratum* MacLeay, 1873.

DIAGNOSIS: The species of *Brithysternum* are clearly differentiated from other broscine genera by a marked posterior projection on the prosternum.

DESCRIPTION: External morphology (figs. 263, 264): Head with one supraorbital seta each side; vertex without posterior transverse groove; temporal ridge complete; antenna with antennomeres 1–2 glabrous, 3–4 with apical ring of setae; 5–11 setose on apical region. Mandibles with scrobal setae. Maxillary eustipes with two or three basal setae; maxillary palpomere 2 and 3 with setae. Labium with submentum bisetose; mentum as-



Figs. 263–274. *Brithysternum calcaratum*: **(263)** head and prothorax; **(264)** mouthparts, ventral view; (**265**) sternum 9, ventral view; (**266**) lateral view; (**267**) left paramere; (**268**) right paramere; (**269, 270**) median lobe, lateral views; (**271**) lateral view, showing internal sac; (**272**) female genital tract, ventral view; (**273**) lateral view; (**274**) spermatheca. See appendix 2 for abbreviations.

etose, without tooth; prementum with glossal sclerite bisetose, ventral surface markedly keeled longitudinally; labial palpomere 2 with four setae. Pronotum not constricted apically, with two or three setae each side; prosternum with a marked projection posteriorly. Elytron with parascutellar striole joined to apical portion of stria 1; with par-

ascutellar seta on basal portion of second stria; lateral umbilical series with 6 to 14 setae. Foreleg trochanter with one seta; foretibia not prolonged externally to apex; male fore and middle tarsomeres without adhesive vestiture, asymmetric.

Male genitalia (figs. 265–271): Sternum 9 with complete ring, with a portion not sclerotized, and lateral margins narrow (figs. 265, 266). Median lobe with dorsal surface membranous (figs. 269, 271); basal orifice completely open dorsally (fig. 269, bo). Internal sac without sclerites X, Y, and apical plate; armature of internal sac with a sclerotized tooth near apical orifice (figs. 270, 271, th) and a broad sclerite (fig. 271). Left paramere asetose (fig. 267); right setose on apical half (fig. 267).

Female genital tract (figs. 272–274): Rami of gonocoxite 9 absent. Subgonocoxite 9 long; gonopod 9 long and sharp, without nematiform setae on subapical setose organ. Spermatheca thin, with accessory gland (fig. 274, acg); median oviduct and spermatheca enter separately into bursa copulatrix; helminthoid sclerite absent; bursa copulatrix short, without accessory gland; ligula sclerotized.

Geographical Distribution: The three species of the genus *Brithysternum* occur in Australia, distributed from northwest (north coast of Western Australia), Northern Territory, to northeastern coast of Queensland.

Material Examined: *Brithysternum calcaratum* (MCZ); *B. macleayi* (ANIC, MCZ).

Cascellius Curtis, 1839

Figures 275–281

Cascellius Curtis, 1839: 185. Waterhouse, 1841b: 255. Gemminger and Harold, 1868: 254. Philippi, 1887: 637. Bruch, 1911: 162. Csiki, 1928: 13. Blackwelder, 1944: 28. Roig-Juñent, 1995a: 56.

Cascelius: Putzeys, 1868: 352 (lapsus). Semenov, 1900: 80. Enderlein, 1912: 61. Schweiger, 1959: 3.

Type Species (subsequent designation, Roig-Juñent 1995): *Cascellius gravesii* Curtis, 1839.

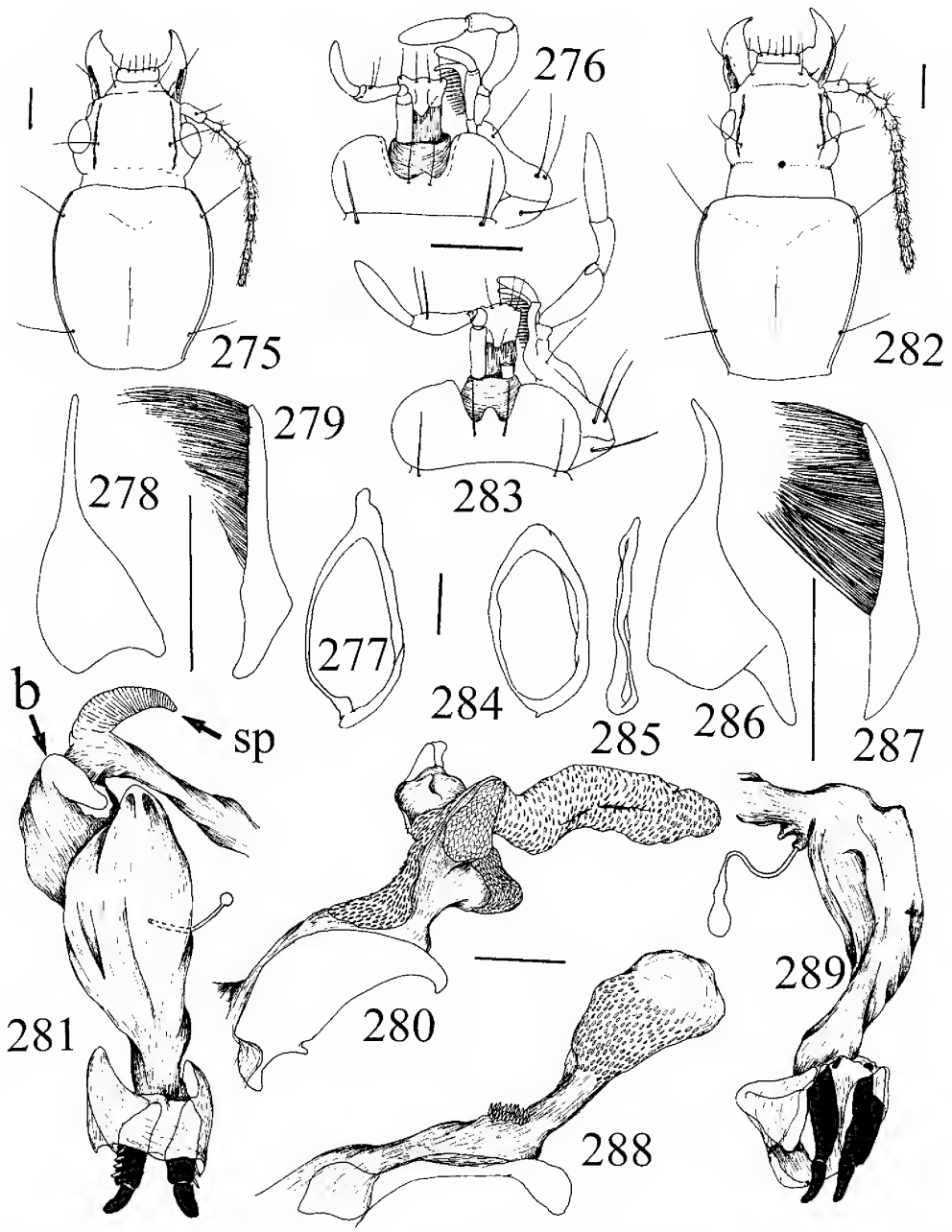
Diagnosis: *Cascellius* belongs to a natural group that has the glossal sclerite quadrisetose as the exclusive feature. Within this group, it differs from *Bountya*, *Nothocascellius*, *Anheterus*, and *Acallistus* in having male middle tarsomeres with adhesive vestiture; from *Creobius* in having only one supraorbital setae on each side; and from *Promecoderus* in having submentum bisetose.

Description: External morphology (figs. 275, 276): One supraorbital puncture each side bearing one seta on each side of head; vertex with transverse groove; temporal ridge complete; antenna with antennomeres 1, 2 glabrous, 3 setose on apical half, 4–11 pubescent all along surface. Mandible each with scrobal setae. Maxillary eustipes with two basal setae; maxillary palpomere 2 asetose. Labium with submentum bisetose; mentum bisetose, with tooth simple, small; prementum with glossal sclerite quadrisetose, ventral surface without longitudinal medial carina, with the paramedian areas deep-set; labial palpomere 2 bisetose. Pronotum not constricted apically, with two setae each side. Elytron with parascutellar striole isolated from apical portion of stria 1; with parascutellar setae on basal portion of second stria; lateral umbilical series with three to five setae. Abdominal sterna 5–8 with a transverse sulcus, shallow in the middle. Foretrochanter with two setae; male with foretarsomeres 1–4 and middle tarsomeres 1–2 with adhesive vestiture ventrally.

Male genitalia (figs. 277–280): Sternum 9 with complete sclerotized ring with lateral margins narrow (fig. 277). Median lobe with dorsal surface unsclerotized (fig. 280) and basal orifice completely open dorsally. Internal sac without sclerite X, Y, and apical plate; armature of groups of small spiculae (fig. 280). Left paramere asetose (fig. 278), right paramere with long hairs from the middle (fig. 279).

Female genital tract (fig. 281): Rami of gonocoxite 9 absent. Subgonocoxite 9 broad, with setae; gonopod 9 short, without nematiform setae on subapical setose organ. Spermatheca broad, with base wide (fig. 281, sp); median oviduct and spermatheca joined before entering into bursa copulatrix; helminthoid sclerite absent; Bursa copulatrix long, with accessory gland in the central region; ligula not sclerotized. Median oviduct with one bursa (fig. 281, b).

Habitat: The species of *Cascellius* live in wet areas of *Nothofagus* forest. *Cascellius*



Figs. 275–289. *Cascellius* and *Nothocascellius*. **(275–281)** *Cascellius gravesii*: (**275**) head and prothorax; (**276**) mouthparts, ventral view; (**277**) sternum 9, ventral view; (**278**) left paramere; (**279**) right paramere; (**280**) median lobe, lateral view, showing internal sac; (**281**) female genital tract, ventral view. (**282–289**) *Nothocascellius hyadesii*. (**282**) head and prothorax; (**283**) mouthparts, ventral view; (**284**) sternum 9, ventral view; (**285**) lateral view; (**286**) left paramere; (**287**) right paramere; (**288**) median lobe, lateral view, showing internal sac; (**289**) female genital tract, ventral view. See appendix 2 for abbreviations.

gravesii is the third most frequent carabid beetle in Tierra del Fuego.

GEOGRAPHICAL DISTRIBUTION: The two species of the genus *Cascellius* occur in southern South America, in Patagonia.

MATERIAL EXAMINED: *C. gravesii* (AMNH, IADIZA, MCZ, USNM) and *C. septentrionalis* (AMNH, IADIZA).

Nothocascellius Roig-Juñent, 1995

Figures 282–289

Cascellius Curtis, 1839: 185 (part). Waterhouse, 1841: 255. Gemminger and Harold, 1868 (part): 244. Bruch, 1911 (part): 162. Germain, 1911 (part): 53. Csiki, 1928 (part): 13. Blackwelder, 1944 (part): 28.

Cascelius: Putzeys, 1868 (lapsus) (part): 352. Kolbe, 1907 (part): 40. Enderlein, 1912 (part): 61. Schweiger, 1959 (part): 3.

Nothocascellius Roig-Juñent, 1995a: 59.

TYPE SPECIES (by original designation): *Cascellius aeneoniger* Waterhouse, 1841.

DIAGNOSIS: *Nothocascellius* belongs to the same group as does *Cascellius*. It differs from *Creobius* in having one supraorbital setae, from *Cascellius* in lacking middle tarsal adhesive vestiture, from *Bountya* in having foretarsal adhesive vestiture, and from the Australian cerobiine genera in having submentum bisetose.

DESCRIPTION: External morphology (figs. 282–283): One supraorbital puncture bearing one seta each side of head; vertex with transverse groove and a central fovea; temporal ridge distinct at apical region; antenna with antennomeres 1–2 glabrous, 3 setose on apical half, 4–11 pubescent all along surface. Mandible each with scrobal setae. Maxillar eustipes with two basal setae; maxillary palpomere 2 asetose. Labium with submentum bisetose; mentum bisetose, with tooth simple; prementum with glossal sclerite quadrisetose apically, ventral surface without longitudinal medial carina, with the paramedian areas deep-set; labial palpomere 2 bisetose. Pronotum not constricted apically, with two setae each side. Elytron with parascutellar striole isolated from apical portion of stria 1; with parascutellar seta on basal portion of second stria; lateral umbilical series with three to five setae. Abdominal sterna 5–8 with a transverse sulcus. Foreleg trochanter with one or two setae; male foretarsomeres 1–2 or 1–3 with adhesive vestiture ventrally, middle tarsomeres without it.

Male genitalia (figs. 284–288): Sternum 9 with complete sclerotized ring with lateral margins narrow (figs. 284–285). Median lobe with dorsal surface lobe unsclerotized (fig. 288), and basal orifice completely open dorsally. Internal sac without sclerite X, Y, and apical plate; armature of small group of spiculae in apical orifice (fig. 288). Left paramere setose (two setae in *N. aeneoniger*) or asetose (fig. 286); right paramere with long hairs from basal third (fig. 287).

Female genital tract (fig. 289): Rami of gonocoxite 9 small. Subgonocoxite 9 broad, with setae; gonopod 9 short, without nematiform setae on subapical setose organ. Median oviduct and spermatheca enter separately into bursa copulatrix; helminthoid sclerite absent. Bursa copulatrix long, without accessory gland.

HABITAT: Species of this genus are found in the most humid and austral habitats in the *Nothofagus* forest and the Magellan moorland. *N. hyadessi* also inhabits oceanic islands south of Tierra del Fuego.

GEOGRAPHICAL DISTRIBUTION: The species of the genus *Nothocascellius* occur in Patagonia, southern South America.

MATERIAL EXAMINED: *N. aeneoniger* (AMNH, IADIZA, MCZ); *N. hyadessi* (AMNH, MCZ, USNM).

Bountya Townsend, 1971

Bountya Townsend, 1971: 180.

TYPE SPECIES (BY MONOTYPY): *Bountya insularis* Townsend, 1971.

DIAGNOSIS: *Bountya* belongs to the same group as *Cascellius*. *Bountya* and *Anheterus* are the only genera that male have foretarsomeres without adhesive vestiture. It differs from *Anheterus* in having 9–12 setae on lateral umbilical series.

DESCRIPTION (after Townsend, 1971): External morphology: One supraorbital seta bearing one seta at each side of head; vertex without transverse groove; antenna with antennomere 2 glabrous, 3 pubescent on apical third, 4 on apical half, 5–11 all along surface. Mandible with or without scrobal setae. Labium with submentum having eight setae; tooth of mentum simple; prementum with glossal sclerite quadrisetose. Pronotum not constricted apically, with two setae each side.

Elytron with parascutellar seta on basal portion of second stria; lateral umbilical series with 9–12 setae. Abdominal sterna smooth. Male fore and middle tarsomeres without adhesive vestiture.

Male genitalia: Median lobe with dorsal surface unsclerotized and basal orifice completely open dorsally. Internal sac without sclerite X, Y, and apical plate. Left paramere asetose, with apical region thin; right setose.

Female genital tract: Subgonocoxite 9 broad; gonopod 9 short, without nematiform setae on subapical setose organ. Median oviduct and spermatheca entering separately into bursa copulatrix; helminthoid sclerite absent, bursa copulatrix long.

LARVAE: The larva was described by Townsend (1988).

DISTRIBUTION AND HABITAT: The genus *Bountya* occurs in Bounty Island, south of New Zealand, occupying a subantarctic habitat.

Creobius Guérin-Ménéville, 1838

Figures 290–297

Feronia (Creobius) Guérin-Ménéville, 1838: 4.
Creobius: Waterhouse, 1841b: 255. Solier, 1849: 200. Semenov, 1900: 80. Csiki, 1928: 14. Blackwelder, 1944: 28. Schweiger, 1959: 3. Roig-Juñent, 1995a: 53.
Cascellius Curtis, 1839 (part): 183. Waterhouse, 1841: 254. Gemminger and Harold, 1868: 244. Waterhouse, 1881: 80. Philippi, 1887: 637. Bruch, 1911: 162. Germain, 1911: 53.
Cascelius Putzeys, 1868 (part) (lapsus): 352.

TYPE SPECIES (by monotypy): *Feronia* (*Creobius*) *eydouxii* Guérin-Ménéville, 1838.

DIAGNOSIS: *Creobius* belongs to the same group as *Cascellius*, and differs from all the genera of this group in having three or more supraorbital setae on each side.

DESCRIPTION: External morphology (figs. 290, 291): Three to five supraorbital punctures bearing one seta each side of head; vertex without transverse groove; temporal ridge obsolete in middle; antenna with antennomeres 1–2 glabrous, 3 setose on half or apical third, 4–11 pubescent all along surface. Mandible each with scrobal setae. Maxillary eustipes with two basal setae; maxillary palpomere 2 asetose. Labium with submentum bisetose; mentum bisetose, with tooth simple; prementum with glossal sclerite quadrisetose, ventral surface without longitudinal medial carina, with the paramedian areas deep-set; labial palpomere 2 bisetose. Pronotum not constricted apically, with five to six setae each side. Elytron with parascutellar striole joined to apical portion of stria 1; with parascutellar seta on basal portion of second stria; lateral umbilical series with 9 to 12 setae. Foretrochanter with one setae; male foretarsomeres 1–4 and middle tarsomeres 1–2 with adhesive vestiture ventrally.

Male genitalia (figs. 292–296): Sternum 9 with complete ring, having a portion not sclerotized, and lateral margins narrow (figs. 292, 293). Median lobe with dorsal surface unsclerotized and basal orifice completely open dorsally (fig. 296). Internal sac without sclerite X, Y, and apical plate; armature of small spiculae (fig. 296). Left paramere asetose (fig. 294); right paramere with long hairs from the middle (fig. 296).

Female genital tract (fig. 297): Rami of gonocoxite 9 short. Subgonocoxite 9 broad, without setae; gonopod 9 short, without nematiform setae on subapical setose organ. Spermatheca broad (fig. 297, sp); median oviduct and spermatheca enter separately into bursa copulatrix; helminthoid sclerite absent. Bursa copulatrix long, with apical accessory gland (fig. 297), without basal sclerite; ligula not sclerotized.

DISTRIBUTION AND HABITAT: The genus *Creobius* has a single species restricted to the northern *Nothofagus* forest of Argentina and Chile, being one of the most common carabid species in this area.

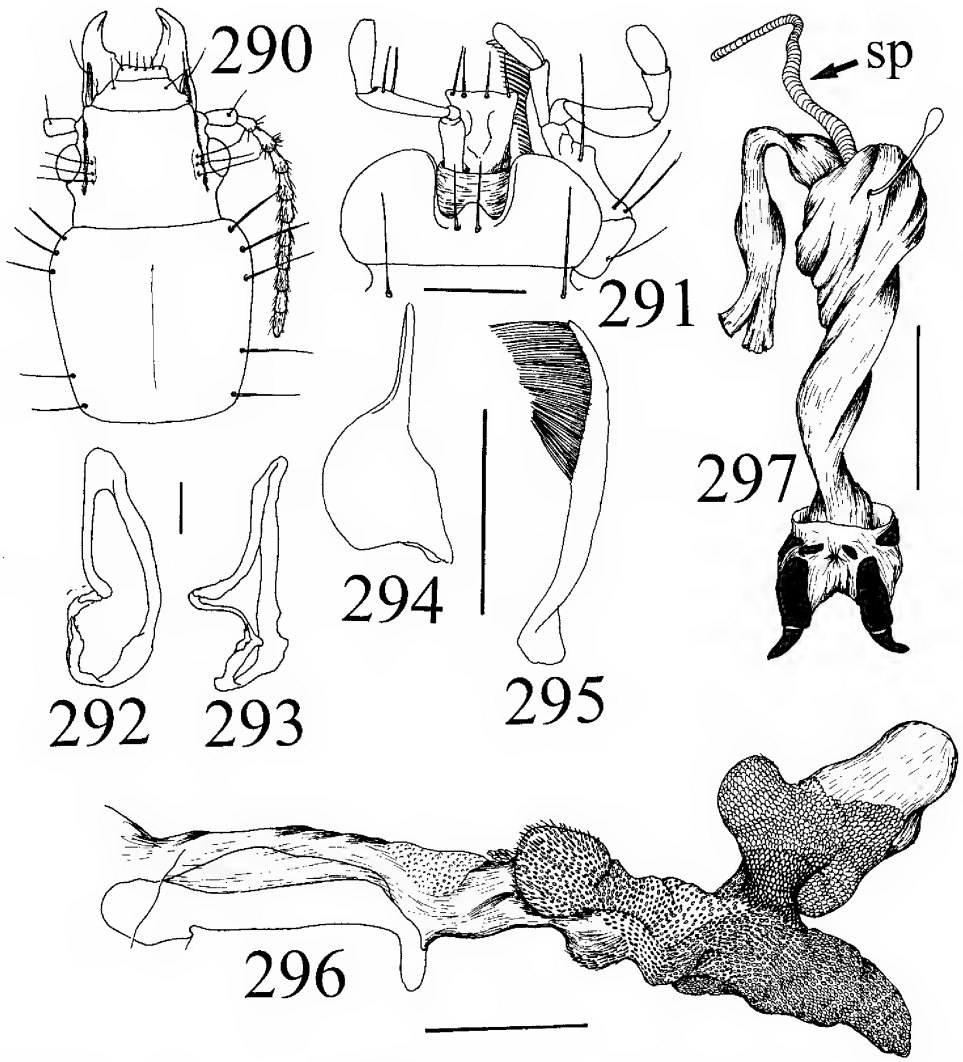
MATERIAL EXAMINED: *Creobius eydouxii* (AMNH, CM, CUIC, IADIZA, MCZ, USNM).

Promecoderus Dejean, 1829

Figures 298–325

Promecoderus Dejean, 1829: 25. Waterhouse, 1842: 205. Lacordaire, 1854: 244. Putzeys, 1868: 328; 1873: 319. MacLeay, 1873: 330. Sloane, 1890: 190; 1920: 124. Csiki, 1928: 24. Lawrence et al., 1987: 109.
Cnemacanthus Gray, 1832: 276 (type species *Cnemacanthus gibbosus* Gray, 1832 by monotypy).

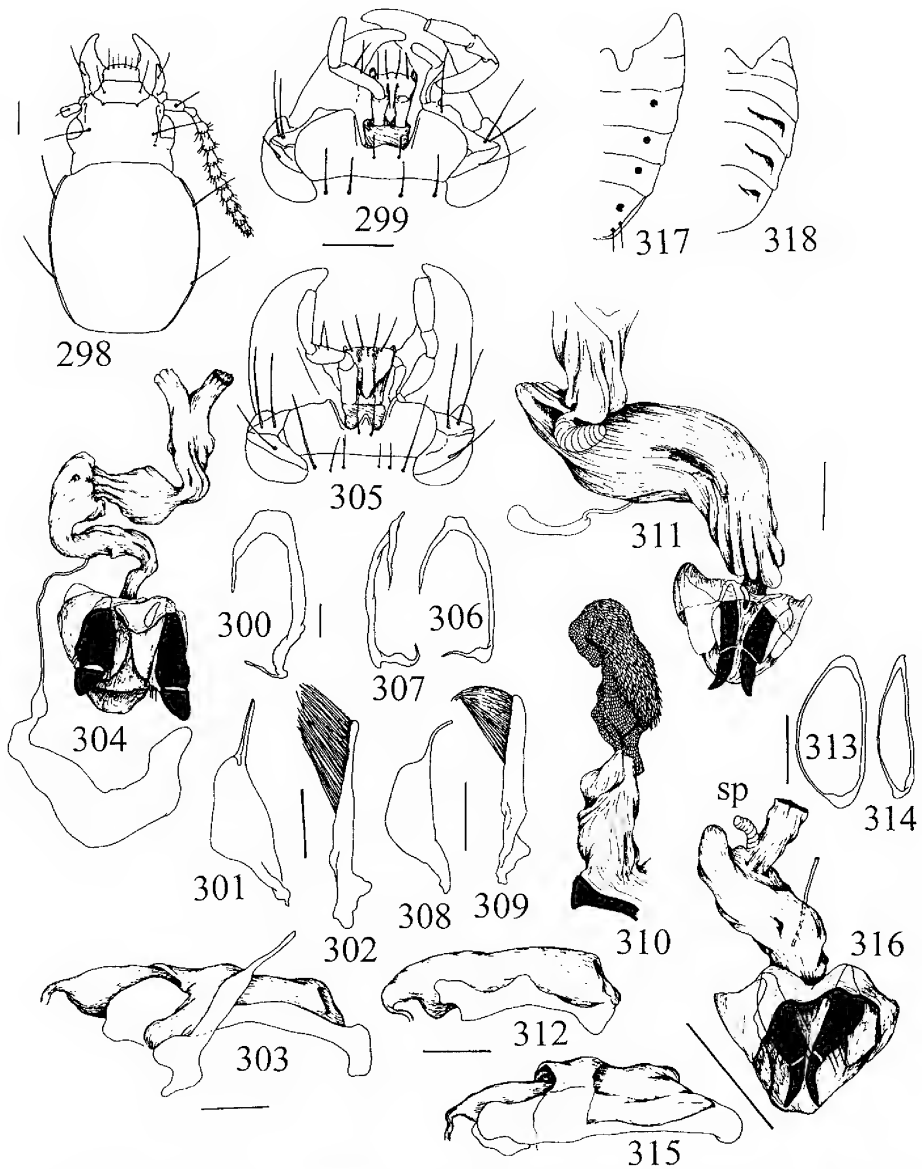
TYPE SPECIES (by monotypy): *Promecoderus brunnicornis* Dejean, 1829.



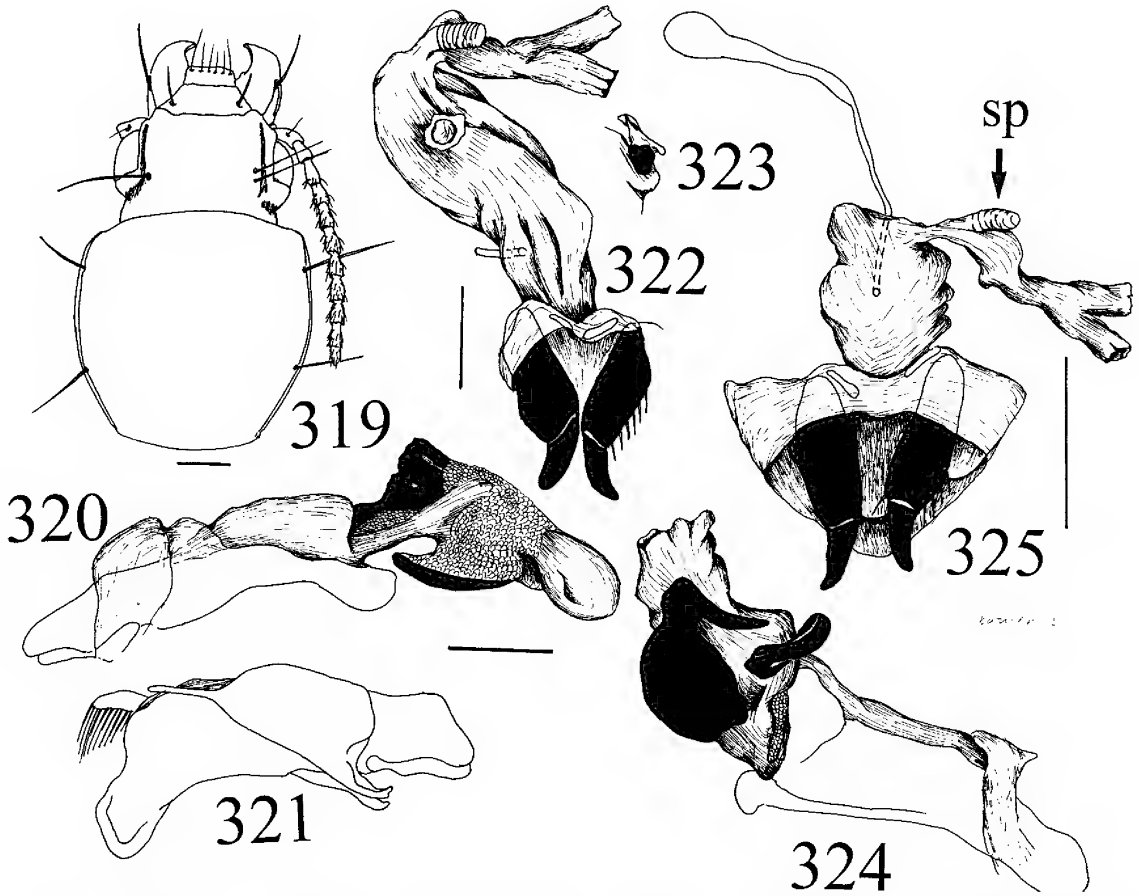
Figs. 290–297. *Creobius eudouxy*. (**290**) Head and prothorax; (**291**) mouthparts, ventral view; (**292**) sternum 9, ventral view; (**293**) lateral view; (**294**) left paramere; (**295**) right paramere; (**296**) median lobe, lateral view, showing internal sac; (**297**), female genital tract, ventral view.

DIAGNOSIS: *Promecoderus* belongs to the same group as does *Cascellius*, and is characterized by the following combination of characters: submentum with four to six setae, lateral umbilical series with four setae, and fore and middle male tarsomeres with adhesive vestiture.

DESCRIPTION: External morphology (figs. 298, 299, 305, 317–319): One supraorbital puncture bearing one seta on each side of head; vertex with or without transverse groove; temporal ridge complete or absent from middle; antenna with antennomeres 1–2 glabrous, 3 with apical ring or setose on apical half, 4 setose on apical half or complete setose, 5–11 pubescent all along surface. Mandibles with scrobal setae. Maxillary eustipes with two basal setae; maxillary palpomere 2 asetose. Labium with four to six setae on submentum; mentum bisetose, with tooth simple, small; prementum with glossal sclerite quadrisetose, ventral surface without longitudinal medial carina, with paramedian areas deep-set; labial palpomere 2 bisetose. Pronotum not constricted apically, with two setae each side. Elytron with parascutellar



Figs. 298–318. *Promecoderus*. (**298–304**), group A, *Promecoderus brunnicornis*: (**298**) head and prothorax; (**299**) mouthparts, ventral view; (**300**) sternum 9, ventral view; (**301**) left paramere; (**302**) right paramere; (**303**) median lobe, lateral view; (**304**) female genital tract, ventral view. (**305–312**) Group B, *Promecoderus howitti*: (**305**) mouthparts, ventral view; (**306**) sternum 9, ventral view; (**307**) lateral view; (**308**) left paramere; (**309**) right paramere; (**310**), apex of median lobe, lateral view showing internal sac; (**311**) female genital tract, ventral view; (**312**) *Promecoderus lucidicollis*, median lobe, lateral view. (**313–316**) Group C, *Promecoderus dischiroides*: (**313**) sternum 9, ventral view; (**314**) lateral view; (**315**) median lobe, lateral view; (**316**) female genital tract, ventral view. (**317**) Sternites of *Promecoderus clivinoides*; (**318**) sternites of *Promecoderus gibbosus*.



Figs. 319–325. *Promecoderus*. (**319–323**), group E, *Promecoderus gibbosus*: (**319**) head and prothorax; (**320**) median lobe, lateral view showing internal sac; (**321**) median lobe, lateral view showing inversion of parameres, (**322**) female genital tract, ventral view; (**323**) ligula of female genital tract. (**324, 325**) Group D, *Promecoderus albaniensis*: (**324**) median lobe, lateral view showing the internal sac; (**325**) female genital tract, ventral view.

striole joined to apical portion of stria 1; with parascutellar seta on basal portion of second stria; lateral umbilical series with four setae. Abdominal sterna 4–7 smooth, with two lateral foveae each side (fig. 317) or extended mediad as a groove (fig. 318). Foretrochanter bisetose; male foretarsomeres 1–4 or 1–3 and middle tarsomeres 1–2 with adhesive vestiture ventrally.

Male genitalia (figs. 300–303, 306–310, 312–315, 320–321, 324): Sternum 9 with complete sclerotized ring (fig. 313, 314) or incomplete (figs. 300, 306, 307) with lateral margins narrow. Median lobe with dorsal surface unsclerotized and basal orifice completely open dorsally (figs. 303, 312, 315, 321, 324). Internal sac without sclerite X, Y, and apical plate; armature of groups of small spiculae (figs. 310, 320), in some species with a sclerotized plate near the middle (figs. 324). Left paramere asetose (figs. 301, 308); right setose (figs. 302, 309). Some species exhibit an inversion of the aedeagus (figs. 321) that renders the left paramere setose and the right asetose.

Female genital tract (figs. 304, 311, 316, 322, 323, 325): Rami of gonocoxite 9 small. Subgonocoxite 9 broad, with ensiform setae; gonopod 9 short and broad, without nematiform setae on subapical setose organ. Spermatheca broad (figs. 311, 316, 322, 325, sp); median oviduct and spermatheca enter to-

gether (figs. 311, 322) or separated into bursa copulatrix; helminthoid sclerite absent. Bursa copulatrix long; ligula sclerotized (figs. 323) or not.

LARVAE: The larva of *P. concolor* was described by Moore (1964).

HABITAT: The species of *Promecoderus* occupy different habitats, ranging from the rainforest (*Nothofagus*) to dry open woodland (Darlington, 1961; Lawrence et al., 1987) or dry sclerophyll zone and open scrub (Sloane, 1890; Lawrence et al., 1987).

GEOGRAPHICAL DISTRIBUTION: *Promecoderus* occurs in Tasmania and southeastern Australia.

REMARKS: The genus *Promecoderus* is one of the most diverse broscine genera, with 44 species, and there is no clear synapomorphy of the group. For this reason, I treat the genus as five different groups of species in attempting to prove the monophyly of *Promecoderus*. This genus needs a full revision. I consider only those species in which males have an adhesive vestiture ventrally on fore and middle tarsomeres 1 and 2 as belonging to *Promecoderus*. The species considered as a Tasmanian group by Sloane (with adhesive vestiture on foretarsomeres and without it on the middle tarsomeres) are considered here as belonging to *Acallistus*. The species without adhesive vestiture on fore and middle tarsomeres are considered here as belonging to *Anheterus*.

MATERIAL EXAMINED: The species studied, arranged by natural groups proposed by Sloane (1890), are as follows:

Group A, *brunnicornis* group (figs. 300–306): *P. brunnicornis* (MCZ). This group is characterized by the presence of a row of setae on male sterna 4–7 and two setae each side of sternum 8.

Group B, *concolor* group (figs. 307–314): *P. concolor* (AMNH). This group is characterized by elytra smooth, and male foretarsomeres 1-3 with adhesive vestiture ventrally. Other characters are: no row of setae on male sterna 4–7 and sternum 8 with one setae each side.

Group C, *clivinoides* group (figs. 315–318): *P. comes* (AMNH), *P. dyschiroides* (MCZ) and *P.* aff. *clivinoides* (AMNH). This group is characterized by: no row of setae on male sterna 4–7; one setae each side of sternum 8; elytra striate; male foretarsomeres 1–4 slender, with adhesive vestiture ventrally.

Group D, *albaniensis* group (figs. 326–327): *P. albaniensis* (AMNH; MCZ). This group is characterized by no row of setae on male sterna 4–7; one setae each side of sternum 8; elytra striate; abdominal sterna 4–7 with deep rounded lateral foveae, without a transverse sulcus; male foretarsomeres 1–4 broad, with adhesive vestiture ventrally.

Group E, *gibbossus-subdepressus-inornatus* group (figs. 321–325): *P. subdepressus* (AMNH), *P. gibbosus* (MCZ, USNM), *P.* aff. *elegans* (AMNH), *P. inornatus* (MCZ). This group is easily recognized because its species have foveo-sulci on abdominal sterna 4–7, a prominent sulcus dorsally posterior to the eyes, and a sclerotized plate in the internal sac. Also some species of this group have the aedeagus inverted (fig. 321), where the left paramere has the shape and setae of the right, and the right is asetose and with the shape of the left.

Acallistus Sharp, 1886

Figures 326–335

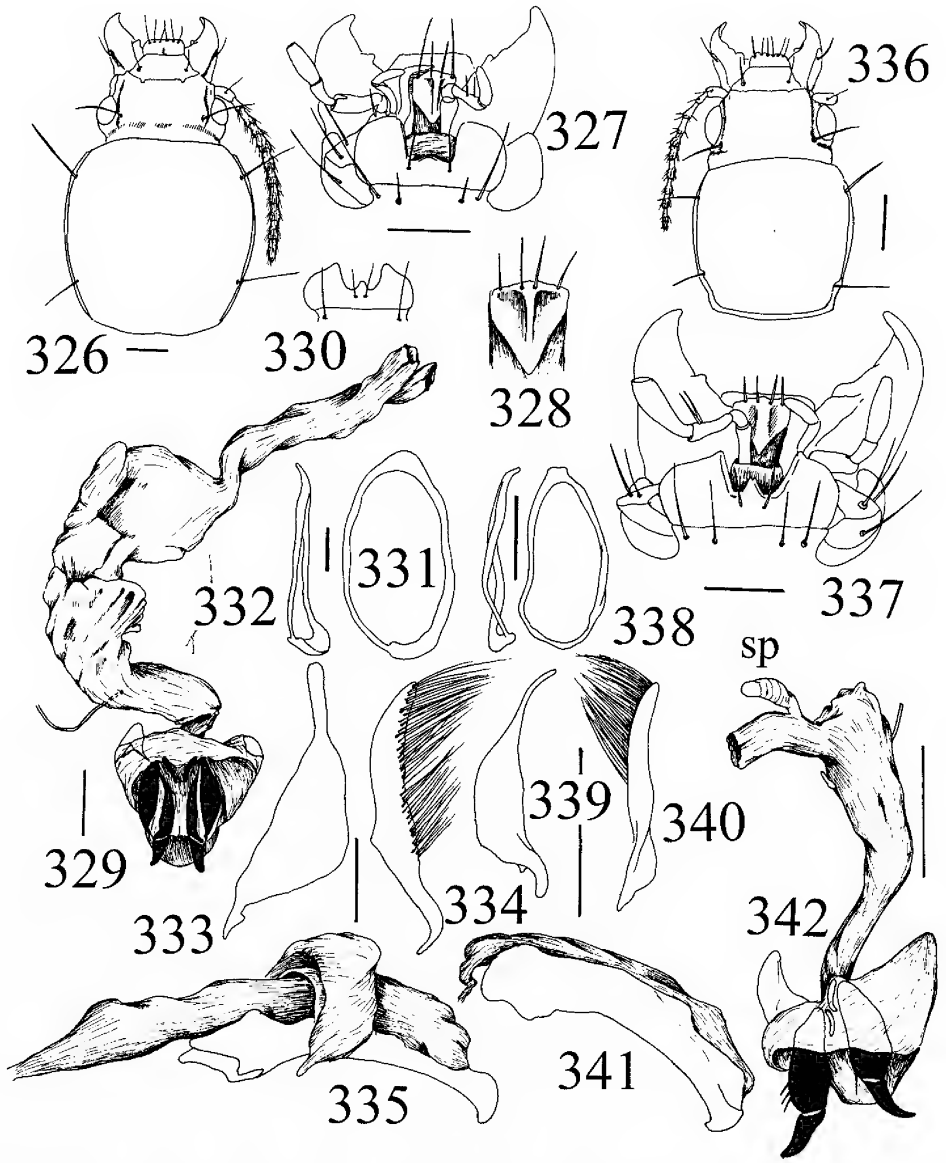
Acallistus Sharp, 1886: 362. Broun 1893: 983. Sloane, 1920: 127.

Promecoderus: Britton, 1949: 537. Lawrence et al. (part), 1987: 109.

TYPE SPECIES (by monotypy): *Acallistus simplex* Sharp, 1886 (junior synonym of *Promecoderus tasmanicus* Castelnau, 1867).

DIAGNOSIS: *Acallistus* belongs to the same group as does *Cascellius*. It differs from South American creobiines in having submentum quadrisetose, from *Bountya* and *Anheterus* in having male foretarsomeres with adhesive vestiture, and from *Promecoderus* in lacking adhesive vestiture on middle tarsomeres.

DESCRIPTION: External morphology (figs. 326–328, 330): One supraorbital puncture each side bearing one seta on each side of head; vertex with shallow transverse groove; temporal ridge complete or absent from middle; antenna with antennomere 1 and 2 glabrous, 3 with apical ring of setae, 4 setose on apical half, 5–11 setose all along surface. Mandibles each with scrobal setae. Maxillary eustipes with two basal setae; maxillary palpomere 2 asetose. Labium submentum quad-



Figs. 326–342. *Acallistus* and *Anheterus*. (**326–342**) *Acallistus plebius*: (**326**) head and prothorax; (**327**) mouthparts, ventral view; (**328**) ligula, ventral view; (**329**) female genital tract, ventral view. (**330–335**) *Acallistus longus*: (**330**) mouthparts, ventral view; (**331**) sternum 9, ventral view; (**332**) lateral view; (**333**) left paramere; (**334**) right paramere; (**335**) median lobe, lateral view. (**336–342**) *Anheterus gracilis*: (**336**) head and prothorax; (**337**), mouthparts, ventral view; (**338**) sternum 9, ventral view; (**339**) left paramere; (**340**) right paramere; (**341**) median lobe, lateral view; (**342**) female genital tract, ventral view.

risetose; mentum tooth reduced to a small convexity (*A. tasmanicus*, *A. plebius*) (fig. 327) or distinctly developed (*A. longus*) (fig. 330); prementum with glossal sclerite quadrisetose, ventral surface without longitudinal medial carina, with the paramedian areas deep-set (fig. 328); labial palpomere 2 bisetose. Pronotum not constricted apically, with two setae each side. Elytron with parascutellar striole joined to apical portion of stria 1; with parascutellar seta on basal portion of second stria; lateral umbilical series with four

setae. Abdominal sterna 4–7 smooth, with a shadow of lateral fovea. Foreleg trochanter bisetose; male foretarsomeres 1–3 or 1–4 with adhesive vestiture ventrally; middle tarsomeres without it.

Male genitalia (figs. 331–335): Sternum 9 with a complete ring, a portion not sclerotized, and lateral margins narrow (figs. 331, 332). Median lobe with dorsal surface unsclerotized and basal orifice completely open dorsally (fig. 335). Internal sac without sclerite X, Y, and apical plate. Left paramere asetose (fig. 333); right setose on two apical thirds (fig. 334).

Female genital tract (fig. 329): Rami of gonocoxite 9 short. Subgonocoxite 9 broad, with ensiform setae; gonopod 9 short, without nematiform setae on subapical setose organ. Median oviduct and spermatheca entering separately into bursa copulatrix; helminthoid sclerite absent. Bursa copulatrix long; without ligula.

HABITAT: The species inhabit tall forest (Lawrence et al., 1987).

GEOGRAPHICAL DISTRIBUTION: The genus *Acallistus* occurs in Tasmania. Sharp (1886) reported its occurrence in New Zealand, but Britton (1949) stated that this record was erroneous.

REMARKS: The genus was recognized originally for a single species, *Acallistus simplex* Sharp 1886. It was later considered by Britton (1949) as junior synonym of *Promecoderus tasmanicus* Castelnau, 1867. Sloane (1890) revised the genus *Promecoderus*, and stated that *P. tasmanicus* constitutes a natural group together with other species. In this contribution, I consider this group of species as genus *Acallistus*, different from *Promecoderus*.

MATERIAL EXAMINED: *Acallistus tasmanicus* (MCZ), *A. plebius* (NEW COMBINATION) (USNM), *A. longus* (NEW COMBINATION) (MCZ), *A. cuprescens* (NEW COMBINATION) (MCZ), and *A.* aff. *longus* (ANIC).

Anheterus Putzeys, 1868

Figures 336–342

Anheterus Putzeys, 1868: 345; 1873: 337. Csiki, 1928: 23.

Promecoderus: Sloane, 1890 (part): 192; Lawrence et al. (part), 1987: 109.

TYPE SPECIES (by subsequent monotypy in Putzeys, 1868): *Promecoderus gracilis* Germar, 1848.

DIAGNOSIS: *Anheterus* belongs to the same group as does *Cascellius*. *Anheterus* and *Bountya* are the only genera of this group without adhesive vestiture on male foretarsomeres. *Anheterus* differs from *Bountya* in having four setae on lateral umbilical serie.

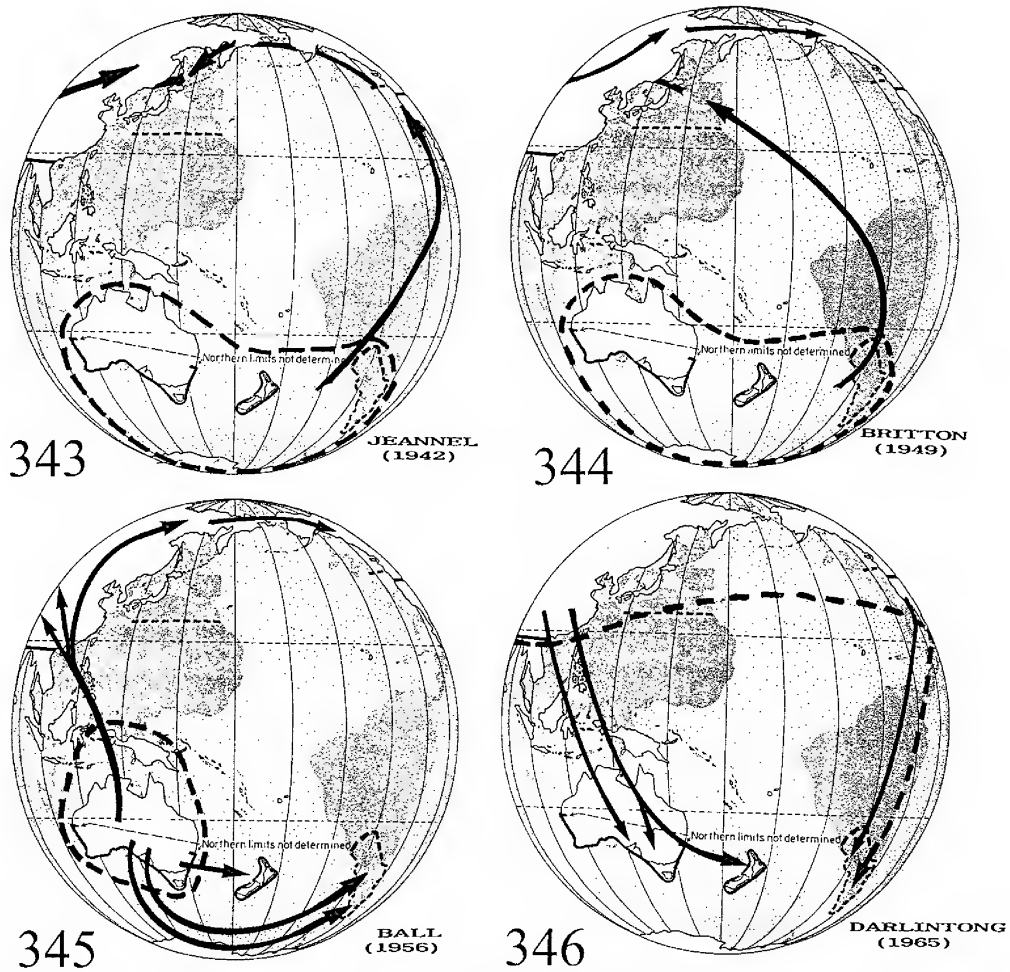
DESCRIPTION: External morphology (figs. 336, 337): One supraorbital puncture bearing one seta on each side of head; vertex without transverse groove; temporal ridge complete; antenna with antennomeres 1–2 glabrous, 3 with apical ring of setae; 4 setose on apical half, 5–11 pubescent all along surface. Mandibles each with scrobal setae. Maxillary with eustipes having two basal setae; maxillary palpomere 2 asetose. Labium with submentum quadrisetose; tooth of mentum simple; prementum with glossal sclerite quadrisetose apically, ventral surface without longitudinal medial carina, with the paramedian areas deep-set; labial palpomere 2 bisetose. Pronotum not constircted apically, with two setae each side. Elytron with parascutellar striole joined to apical portion of stria 1; with parascutellar setae on basal portion of second stria; lateral umbilical series with four setae. Abdominal sterna 4–7 with a lateral foveae each side. Foreleg trochanter bisetose; male fore and middle tarsomeres without adhesive vestiture.

Male genitalia (figs. 338–341): Sternum 9 with sclerotized ring complete with lateral margins narrow (fig. 338). Median lobe with dorsal surface unsclerotized and basal orifice completely open dorsally (figs. 341). Internal sac without sclerite X, Y, and apical plate. Left paramere asetose (fig. 339); right setose on apical two thirds (fig. 340).

Female genital tract (figs. 342): Rami of gonocoxite 9 short. Gonopod 9 short, without nematiform setae on subapical setose organ. Spermatheca broad (fig. 342, sp); median oviduct and spermatheca entering together into bursa copulatrix; helminthoid sclerite absent. Bursa copulatrix long; ligula small, unsclerotized.

HABITAT: The species inhabit open scrub and low open woodland (Lawrence et al., 1987).

GEOGRAPHICAL DISTRIBUTION: The genus



Figs. 343–346. Biogeographic theories explaining Broscini distribution: (**343**) Jeannel, 1942; (**344**) Britton, 1949; (**345**) Ball, 1956; (**346**) Darlington, 1965.

Anheterus occurs in South Australia (Adelaide) and "Northern Territory of Southern Australia" (Sloane, 1892).

REMARKS: This genus, as redefined herein, contains three species, *A. gracilis*, *A. distinctus* (Sloane, 1890), and A. *ambiguous* (Sloane, 1892), considered by Sloane (1890, 1892) as a natural group of species within the genus *Promecoderus*.

MATERIAL EXAMINED: *Anheterus gracilis* (AMNH, ANIC, MCZ).

BIOGEOGRAPHICAL REMARKS

Several hypotheses have been proposed to explain the geographical distribution of Broscini in temperate areas of both Northern and Southern hemispheres. No tropical species have been reported up to now.

1. Jeannel (1942) (fig. 343) postulated that the tribe arose in the austral continent, in West Gondwana during Jurassic time, where several clades evolved. Also in Jurassic time, one of the broscine clades reached Angaraland (a region of Gondwana that now comprises central and western Asia). This region drifted from Gondwana where new forms developed during the Cretaceous. When Angaraland reached and joined continents in Tertiary time, Broscini spread north, west, and east.

2. Britton (1949) (fig. 344) postulated a Cretaceous Paleantarctic origin for Broscini

because of the relatively greater diversity of the Broscini on southern landmasses. Further, he stated that the Broscini probably spread in early Tertiary time from South America through northern Africa to the Palearctic region, by way of a land connection from northern South America to the Mediterranean region. Britton (1949: 535) did not accept the invasion of the Northern Hemisphere through Asia because "the Palaeantarctic continent was separated from Asia from the end of the Jurassic until the late Tertiary so that the Broscini could not have reached Asia directly from Australia sufficiently early to allow for the considerable diversification of the Palearctic genera and species".

3. Ball (1956) (fig. 345) postulated that the tribe arose in southeastern Asia or Australia and dispersed from either of these centers. The ancestral stocks of Barypina and Creobiina reached South America by way of a southern route. He suggested that his data did not support the Broscina reaching the Palearctic continent by way of South America, because this subtribe (at that time) was not represented in South America and the center of abundance of the group seemed to be in the eastern Palearctic region. From the Australian center a group spread northward, possibly by way of what is now the Indo-Australian Archipelago. Open stretches of sea may have been crossed by flight, or by other means, and then across the tropical areas of the Old World to the Himalaya and then farther northward, eastward, and westward. Another group reached New Zealand from Australia, over the sea.

4. Darlington (1965) (fig. 346) proposed a worldwide cycle of evolution and dispersal for amphitropical taxa. The postulated cycle is: rise on the large land masses in the Northern Hemisphere or possibly in the tropics; dispersal southward into southern South America and southern Australia by separate routes, and to New Zealand probably from Australia; disappearance of the tropical or tropics-crossing forms, leaving an amphitropical pattern; and finally disappearance from the Northern Hemisphere, leaving survivors on the three main pieces of land in the southern cold temperate zone.

Darlington suggested that Broscini is younger than other austral groups, because it has moved South more recently and is just beginning to invade the southernmost moorland. Also, some of the northern taxa are winged, as the ancestors of the tribe must have been. However, broscines have evidently been in the Southern Hemisphere for a considerable time, because all the southern genera are different from northern ones, and no genus occurs in more than one of the three main areas of distribution in the south.

Most authors have argued an austral origin of the tribe, and their dispersal to the north, except Darlington (1965), who expressed the opposite idea, and Erwin (1985) who proposed a tropical origin. The phylogenetic hypothesis based on the cladograms obtained here suggests a different explanation from all those mentioned above. Cladograms (figs. 14, 15) together with past land distribution show that it is not necessary to use dispersal from a center of origin to explain this amphitropical distribution. Broscini could be considered a Pangaeic tribe, and the origin of austral and holarctic groups could be due to a separation of Pangaea landmasses. Broscini could have originated in lower Jurassic time when there was a land connection between South America and North America on the Pacific margin (Smith and Briden, 1977). Other amphitropical carabid groups support the existence of this connection (Erwin, 1979)—like Trachypachinae, with *Trachypachus* Motschulsky in western North America and Europe and *Systolosoma* Solier in *Nothofagus* forest of South America. The first split of Broscini generated Axonyina, two genera of which are presently distributed in Asia, and one, *Rawlinsius* in Central America, that corroborate the origin of this group in the Pacific margin of America. The second split of Broscini could be related with the breakup of Pangaea into Laurasia and Gondwana, isolating Broscina, as Holarctic group, from the common ancestor of Barypina, Nothobroscina, and Creobiina. Probably Broscina spread to other regions from North America. This subtribe has some species with great powers of dispersal, like Recent genera *Miscodera*, with its unique species distributed in Europe, Siberia, and North America, and *Broscosoma*, with several species distributed from Europe to Japan.

The austral broscine ancestor was wide-

spread in Western Gondwanaland, in a continuous landmass along the southern margin of the Pacific, from northern Australia along Antarctica to southern South America. The New Zealand microplate is believed to fit along the East Antarctic-Australian craton with the Lord Howe Rise adjacent to northeastern Australia, and the present land area of New Zealand located east of Tasmania (Zinsmeisteir, 1982). The austral broscine ancestor has a great reduction in metathoracic wings (figs. 14, 15, character 36[1]), and for this reason the present distribution of austral Broscini has to be explained by land connections of austral areas. This is not new, because the study of disjunct distributional patterns of extant organisms occurring in southern South America, New Zealand, Australia, and other southern land masses may be best explained by southern continental connections from Triassic to upper Cretaceous times (Dietz et al., 1972; Smith and Hallam, 1970; Harrison et al., 1979; Dalziel, 1983)

It is not possible to find the basis for the first split of two austral broscine groups, except to note that it was before the complete separation of the Campbell Plateau because both groups have species in New Zealand (Creobiina is in Bounty Island).

In broad terms, the biogeographic pattern of Broscini may be explained by the current hypothesis of the breakup of Western Gondwana. The connection of New Zealand with Antarctica was through Marie Byrd Land prior to the subsidence of the Campbell Plateau, in the late Cretaceous (Zinsmeisteir, 1987). New Zealand began its drift away from the Australian-Antarctic margin of Gondwana (Flemming, 1975), and became progressively more isolated about 82 million years ago (Flemming, 1975; Cooper and Millener, 1993), while Australia/Antarctica/South America remained in contact until the Eocene, about 56 million years ago (Flemming, 1975; Drinnan and Crane, 1989). This fact could explain why many taxa from South America have sister groups among taxa distributed in Australia and just a few groups are confined to New Zealand and southern South America, but absent from Australia (Watt, 1975).

Nothobroscina is the most extensive subtribe that occurs in New Zealand. Ball (1956) proposed that the New Zealand genera evolved from a common ancestor, but the cladistic results show that the New Zealand assemblage of Broscini is polyphyletic, evolving from different ancestors. The early separation of New Zealand from the remaining austral areas could explain the basal position of *Diglymma* as sister group of the other Nothobroscina (figs. 14, 15), and the existence of a more related group between Australia and South America, exemplified by *Eurylychnus* and *Nothobroscus*. But this early separation of New Zealand does not explain the close relationship among the other nothobroscine genera distributed in Australia and New Zealand, excluding South American groups (*Chylnus-Oregus* clade, figs. 14, 15).

This particular example of distribution was exhaustively discussed by several authors who proposed an extinction due to different climatic conditions in the different areas for some taxa (Hennig and Wygodzinsky, 1966). However, there is another way to explain this distribution. Besides an early separation of one clade in New Zealand from those in other austral areas, a continuing link between New Caledonia, New Guinea, and Australian groups is proposed. The eastern margins of the Australian plate (New Zealand Plateau, Norfolk Ridge, and Lord Howe Rise) separated from the parent plate more rapidly in the south than in the north, and a tenuous connection with the parent plate was maintained in the North. The existence of two monophyletic groups of Nothobroscina in Australia, like the pattern for other insect taxa, could thus be explained without recourse to dispersal theories (Thornton, 1981). Other arguments that support this northern connection between New Zealand and Australia include the presence of one species of *Percosoma* (*P. asymetricum)*, in New Caledonia. Several other wingless insects of New Caledonia and Lord Howe show a close relationship with the New Zealand fauna, and with eastward landmass fauna in general (Paramonov, 1963). For Paramonov, this evidence supported an ancient connection between Australia and New Zealand by a land bridge, which he called Howeania.

To reconstruct the ancestral habitat, I have mapped and optimized onto the cladogram

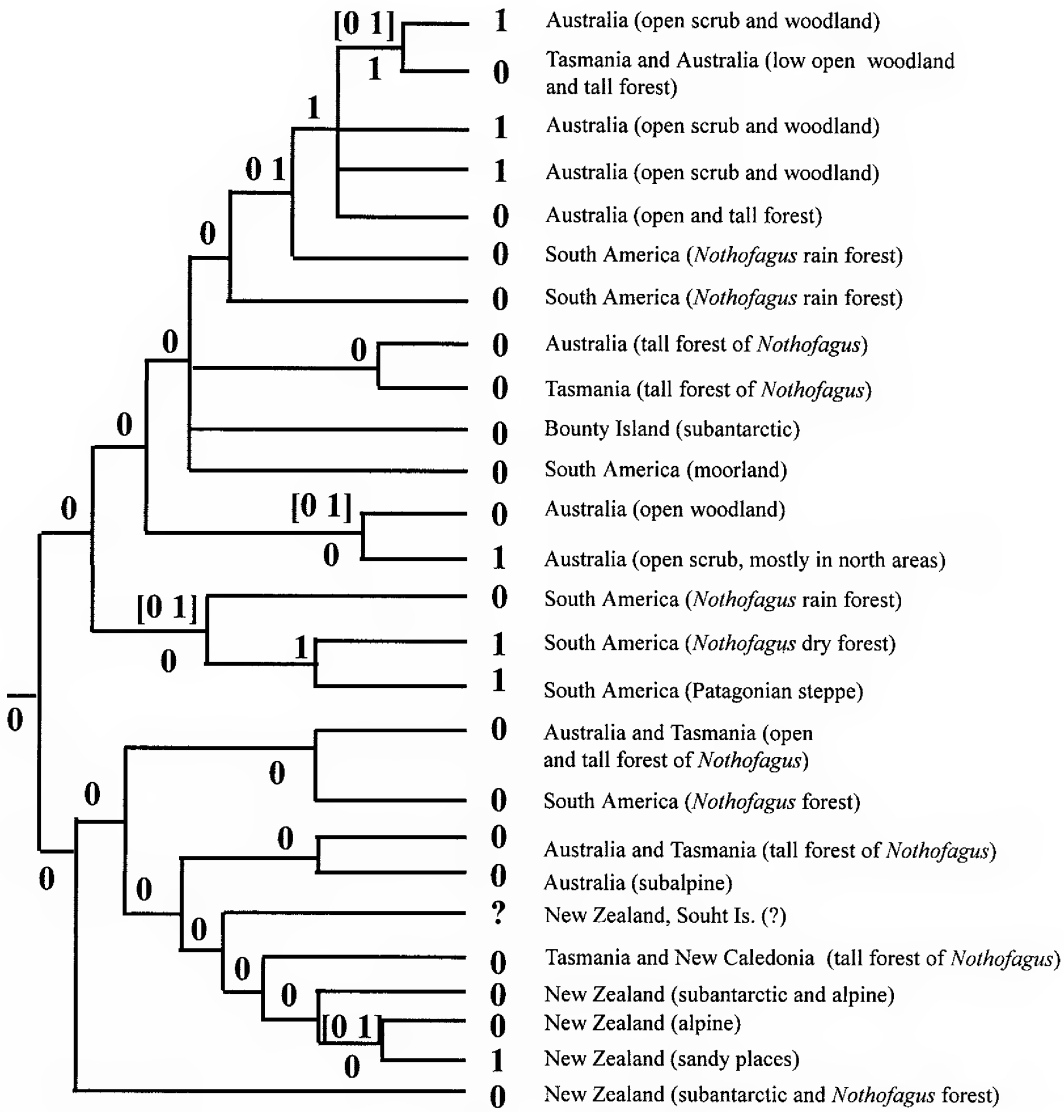

Australia (open scrub and woodland)
Tasmania and Australia (low open woodland and tall forest)
Australia (open scrub and woodland)
Australia (open scrub and woodland)
Australia (open and tall forest)
South America (Nothofagus rain forest)
South America (Nothofagus rain forest)
Australia (tall forest of Nothofagus)
Tasmania (tall forest of Nothofagus)
Bounty Island (subantarctic)
South America (moorland)
Australia (open woodland)
Australia (open scrub, mostly in north areas)
South America (Nothofagus rain forest)
South America (Nothofagus dry forest)
South America (Patagonian steppe)
Australia and Tasmania (open and tall forest of Nothofagus)
South America (Nothofagus forest)
Australia and Tasmania (tall forest of Nothofagus)
Australia (subalpine)
New Zealand, Souht Is. (?)
Tasmania and New Caledonia (tall forest of Nothofagus)
New Zealand (subantarctic and alpine)
New Zealand (alpine)
New Zealand (sandy places)
New Zealand (subantarctic and Nothofagus forest)

Fig. 347. Area cladograms (including habitat distribution) of austral Broscini: Nothobroscina; Barypina; and Creobiina. 0 = humid habitats, 1 = dry habitats.

(fig. 15) the habitat distribution of each genus (fig. 347). Figure 347 shows that the ancestor of Nothobroscina would have inhabited humid places: subantarctic, alpine, or *Nothofagus* forest. According to figure 347, the separation of Creobiina and Barypina occurred before the complete separation of the New Zealand Plateau, because Creobiina remains in Bounty Island (New Zealand). Similar to Nothobroscina, the ancestor of Barypina and Creobiina might have lived in *Nothofagus* forest or humid habitats (subantarctic or moorland). These two tribes show a particular trend. Hennig and Wygodzinsky (1966) noticed that, among taxa common to South America and Australia, a number of forms are associated with dry country, and tend to have a more northern range both in South America and Australia. *Microbarypus* and *Arathymus*, basal taxa in Barypina, lived in *Nothofagus* forest. In South America, the subgenera *Barypus* and *Cardiophthalmus* occupied dry habitats. Basal groups of Creobiina inhabit forestland (figs. 347). Within

Creobiina, the *Cerotalis* clade evolved in Australia and occupied the driest habitat in north Australia. Adults of its species are large—a feature that could be related to arid conditions (Noonan, 1982; Roig-Juñent and Flores, 1995), because it is also typical of *Barypus* species that inhabit driest habitat (Roig-Juñent, 1995b). Also some species of *Promecoderus* are widely distributed across southern Australia, but chiefly in dry forest and arid country (Darlington, 1961).

CONCLUSIONS

Aside from a lack of data about some genera (*Ebertius* and *Sinobrosculus*, and females of *Axonya* and *Broscodes*), I propose a revised reclassification of the tribe Broscini, with a different arrangement of the genera based on external morphological features—typically those of male and female genitalia.

I also present a cladistic analysis that supports the hypothesis that Barypina is derived from the same lineage as was Creobiina, based on the loss of internal structures of female and male genitalia, a synapomorphy of both groups. Within Barypina, the new genus described, *Microbarypus silvicola,* presents several character states that link the subtribes Creobiina and Barypina. Ball (1956) supposed that the loss of the sclerites X and Y occurred several times in different clades, but within Broscini it occurs once. This new classification differs from Jeannel's in that the genera *Miscodera* and *Broscodera* are included in Broscina, and the Australian and New Zealand genera considered as Barypina by Jeannel are considered herein as a new subtribe. It differs from Ball's classification in placing the austral genera with "basal orifice of median lobe close dorsally" in the new subtribe Nothobroscina, and considering that the genera *Broscodes* and *Axonya* constitute a new subtribe, Axonyina.

The cladistic analysis shows that the species of *Promecoderus* do not constitute a monophyletic group, and an exhaustive systematic revision of this genus is needed.

From a biogeographical point of view, the idea of either an austral or Holarctic dispersal center of origin is not supported. The tribe was probably distributed along the Pacific margin during the Jurassic. Some clades are related to the breakup of Pangaea, like the split of the subtribe Broscina from the austral Broscini, due to Laurasia-Gondwana separation. Adults of the ancestor of the austral Broscini were brachipterous, suggesting that an austral area that was split by the drift of the continents circumscribes the present distribution of this austral group.

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APPENDIX 1

Checklist of Broscini taxa. Type species are boldfaced. Species examined are marked with an asterisk.

AXONYINA

Axonya Andrewes, 1923

***Axonya championi** Andrewes, 1923: India

Broscodes Bolívar y Pieltain, 1914

***Broscodes karunamicus** Bolívar y Pieltain, 1914: Iran (Persia)

Rawlinsius Davidson and Ball, 1998

Rawlinsius papillatus Davidson and Ball, 1998: México

BARYPINA

Barypus Dejean, 1828

B. (Arathymus) Guérin-Méneville, 1838

**B. bonvouloiri* Chaudoir, 1861: central Chile

***B. parallelus** (Guérin-Méneville, 1838) (as *Arathymus* subgenus of *Cnemacanthus*): central Chile

= *Odontomerus subsulcatus* Solier, 1849 (taxonomic decision of Putzeys, 1868)

B. (Barypus)

B. aequicostis Chaudoir, 1876: Uruguay

B. calchaquensis Roig-Juñent, 1992b: central Argentina

**B. comechingonensis* Roig-Juñent, 1992b: central Argentina

**B. pulchellus* Burmeister, 1868: pampean region of Argentina

***B. rivalis** (Germar, 1824) (as *Molops*): pampean region of Argentina and Uruguay

B. speciosus Dejean, 1831: Uruguay

B. (Cardiophthalmus)

**B. chubutensis* Roig-Juñent, 1992a: Patagonian steppe

***B. clivinoides** (Curtis, 1839) (as *Cardiophthalmus*): Patagonian steppe

= *Cardiophthalmus stephensi* Waterhouse, 1841a (taxonomic decision of Chaudoir, 1876:124)

= *Tetraodes laevis* Blanchard, 1853 (taxonomic decision of Putzeys, 1868)

B. dentipenis Roig-Juñent, 1992a: Patagonian steppe

B. deplanatus Roig-Juñent and Cicchino, 1989: Patagonian steppe
B. flaccus Roig-Juñent and Cicchino, 1989: Patagonian steppe
B. gentilii Roig-Juñent, 1992a: Patagonian steppe
B. giaii Roig-Juñent, 1992a: Patagonian steppe
**B. longitarsis* (Waterhouse, 1841a) (as *Cardiophthalmus*): Patagonian steppe
**B. mendozensis* Roig-Juñent and Cicchino, 1989: western central Argentina
B. minus Roig-Juñent, 1992a: Patagonian steppe
B. neuquensis Roig-Juñent, 1992a: Patagonian steppe
B. painensis Roig-Juñent and Cicchino, 1989: Patagonian steppe
B. schajovskoii Roig-Juñent, 1992a: Patagonian steppe
B. sulcatipenis Roig-Juñent, 1992b: Patagonian steppe

Microbarypus **new genus**
***Microbarypus silvicola*, new species**: northern *Nothofagus* forest of Chile

BROSCINA

Broscodera Lindroth, 1961a
Broscodera insignis (Mannerheim, 1852), (as *Miscodera*): North America, from Oregon to the southern coast of Alaska

Broscosoma Rosenhauer, 1846
Broscosoma baldense Roshenhauer, 1846: Italian Alps (Monte Baldo)
Broscosoma baldense pasubianum Weissmandl, 1936 (change status by Lindroth 1961a): Italian Alps (Monte Pasubio)
Broscosoma baldense relictum Weissmandl, 1936 (change status by Lindroth 1961a): Italian Alps (Monte Alben)
Broscosoma convexum Deuve, 1983: Nepal
Broscosoma deuvi Lassale, 1982: Nepal
**Broscosoma doenitzi* (Harold, 1881) (as *Miscodera*): Honshu (Japan)
= *Broscosoma elegans* Bates, 1883
Broscosoma gracile Andrewes, 1927: Sikkim (northeast India)
Broscosoma guttuliforme Deuve, 1985: Nepal
Broscosoma monticola Habu, 1973b: Nepal
Broscosoma moriturum Semenov, 1900: Setschuan (West China, pars septentrionalis)
**Broscosoma ribbei* Putzeys, 1877: Darjeeling, Sikkin, northeast India; and Tong-King
Broscosoma schawalleri Deuve, 1990: Nepal Oriental
Broscosoma semenovi Belousov and Katayev, 1990: Caucaso (Stolovaya Mountain, central Caucaso)
Broscosoma sichuanum Deuve, 1990: Sichuan and Songpan (China)
Broscosoma uenoi Habu, 1973a: Formosa (Taiwan)

Broscus Panzer, 1813
B. angustulus Semenov, 1890: China and Turkestan
B. bipilifer Andrewes, 1927: Sikkim (India)
B. cephalotes (Latreille, 1802) (as *Carabus*): north and middle Europe, and Moldova
= *Broscus antennatus* Letzner, 1852
= *Broscus capucinus* Torre, 1879
= *Broscus clypeatus* Letzner, 1852
= *Broscus piceus* Letzner, 1852
= *Broscus rufipes* Letzner, 1852
= *Broscus vulgaris* Fischer, 1823
**B. cephalotes asiaticus* Ballion, 1870: Khodschent
B. cephalotes semistriatus Dejean, 1828: Südrussland
B. costatus Morvan, 1980: Bhutan
B. crassimargo Wollaston, 1865: Canary Islands
**B. davidianus* Fairmaire, 1888: Yunnan, Hong Kong
B. declivis Semenov, 1889: Semirjetschje
B. glaber (Brullé, 1839) (as *Percus*): Canary Islands
= *B. basalis* Newman, 1838: Mexico (the original record probably was an error)
B. insularis Piochard de la Brûlerie, 1867: Baleares Islands
= *B. crenicollis* Schaufus, 1869
B. karelini Zoubkoff, 1837: Transkaspien, Iran, Ferghana
= *B. cordicollis* Chaudoir, 1842
**B. laevigatus* (Dejean, 1828) (as *Cephalotes*): Tunis and Egypt
B. laevigatus illustris Putzeys, 1868 (as var.): Syria and Sinai
**B. nobilis* (Dejean, 1828) (as *Cephalotes*): Kleinasien, Syria, Cyprus, Turkey, and Greece
= *B. ruficeps* (Guérin, 1829) (as *Cephalotes*) (taxonomic decision of Putzeys, 1868)
**B. politus* (Dejean, 1828) (as *Cephalotes*): Sicily, Algeria, and Tunis
= *B. obsoletestriatus* Reitter, 1872 (as aberration)
B. potanini Semenov, 1889: Tibet
**B. przewalskyii* Semenov, 1889: Tibet
**B. punctatus* (Dejean, 1828) (as *Cephalotes*): Sinai, Egypt, Iraq, Arabia, and North India
= *B. limbatus* Ballion, 1870 (taxonomic decision of Andrewes, 1935)
= *B. batesi* Semenov, 1890 (taxonomic decision of Andrewes, 1935)

= *B. nepalensis* (Hope, 1831) (as *Percus*) (taxonomic decision of Andrewes, 1935)
B. rutilans Woll, 1862: Tenerife (Spain)
B. taurulus Andrewes, 1927: Sikkim (India)
B. uhagoni Bolivar y Pieltain, 1912: Toledo (Spain)

Chaetobroscus Semenov, 1899
C. (*Chaetobroscus*)
*__C. anomalus__ (Chaudoir, 1878) (as *Broscus*): Kashmir
C. kezukai Dostal, 1984: Himalaya
C. (*Morvanobroscus*) Dostal, 1984
C. bhutanensis Morvan, 1980: Bhutan

Craspedonotus Schauman, 1863
**C. himalayanus* Semenov, 1910: Himalaya
**C. margellanicus* Kraatz, 1884: Turkestan and Ferghana
= *Pseudobroscus leucocnemis* Semenov, 1888
**__C. tibialis__ Schauman, 1863: Japan, Korea, Manchuria, China (north and central), southern part of Maritime territory of Russia (Kryzhanovskij, 1968)

Eobroscus Kryzhanovskij, 1951
E. (*Eobroscus*)
**__Eobroscus lutshniki__ (Roubal, 1928) (as *Broscus)* (taxonomic decision of Kryzhanovskij, 1951): eastern Asia, Sakhalin, northwestern China, and Japan
= *Eobroscus richteri* Kryzhanovskij, 1951 (taxonomic decision of Kryzhanovskij, 1968)
= *Tosawabroscus amabilis* Uéno, 1953 [nomen nudum] (taken from Morita, 1990)
E. (*Orobroscus*) Morita, 1990
__E. masumotoi__ Morita, 1990: Taiwan
E. bhutanensis Morvan ,1982: Buthan
E. uenoi Morita, 1995: northern Vietnam

Miscodera Eschscholtz, 1830
__Miscodera arctica__ (Paykull, 1798) (as *Scarites*): Finland, Laponia, Sweden, Norway, Scotland, Demmark, northern Germany, Russia, Switzerland; Tirol, Austria, North America: Maine, Lake Superior, Alaska, and Newfoundland.
= *Leiochiton readi* Curtis, 1831
= *Miscodera americana* Mannerheim, 1853
= *Miscodera erythropus* Mothchulsky, 1844
= *Miscodera hardyi* Chaudoir, 1861
= *Miscodera arctica hypsibia* Schauberger, 1934

Sinobrosculus Deuve, 1990
__S. dreuxi__ Deuve, 1990: Sichuan (China)

Zacotus LeConte, 1869
**Zacotus matthewsii* LeConte, 1869: EEUU and Canada
= *Zacotus angustus* Casey, 1920 (taxonomic decision of Ball, 1956)
= *Zacotus subopacus* Hopping, 1925 (taxonomic decision of Ball, 1956)
= *Zacotus fredericki* Nunenmacher, 1944 (taxonomic decision of Ball, 1956)

CREOBIINA

Acallistus Sharp, 1886
**A. cuprescens* (Sloane, 1920) (new combination) (as *Promecoderus*): Tasmania
**A. longus* (Sloane, 1920) (new combination) (as *Promecoderus*): Tasmania
**A. plebius* (Sloane, 1920) (new combination) (as *Promecoderus*): Tasmania
**A. tasmanicus* (Castelnau, 1867) (as *Promecoderus*): Tasmania
= **__A. simplex__** Sharp, 1886 (taxonomic decision Britton, 1949)

Adotela Castelnau, 1867
**A. apicalis* (Sloane, 1893) (as *Parroa*): South Australia, Victoria, and New South Wales
A. atronitens Sloane, 1890: Western Australia and South Australia
A. australis Sloane, 1890: South Australia
**A. bicolor* (Castelnau, 1867) (as *Parroa*): New South Wales (Australia)
A. carbonaria (Castelnau, 1867) (as *Parroa*): Western Australia
A. carenoides Putzeys, 1873: Queensland (Australia)
__A. concolor__ Castelnau, 1867 (present designation as type species): Western Australia
**A. esmeralda* Castelnau, 1867: Western Australia
A. frenchi Sloane, 1890: Western Australia and Northern Territory
A. grandis (Castelnau, 1867) (as *Parroa*): Western Australia
**A. howitti* (Castelnau, 1867) (as *Parroa*): Western Australia and New South Wales
A. laevigatta (Sloane, 1893) (as *Parroa*): Western Australia and South Australia
A. nigerrima MacLeay, 1873: Queensland (Australia)
**A. noctis* (Sloane, 1893) (as *Parroa*): Western Australia
A. striolata Putzeys, 1873: Western Australia
A. violacea (Castelnau, 1867) (as *Parroa*): Western Australia
A. viridis (MacLeay, 1871) (as *Promecoderus*): Queensland (Australia)

Anheterus Putzeys, 1868
A. ambiguus (Sloane, 1892) (new combination) (as *Promecoderus*): South Australia
A. distinctus (Sloane, 1890) (new combination) (as *Promecoderus*): South Australia

*__A. gracilis__ (Germain, 1848) (as *Promecoderus*): South Australia
= *Promecoderus parvulus* MacLeay, 1873 (taxonomic decision of Sloane, 1890)

Bountya Townsend, 1971
__B. insularis__ Townsend, 1971: Bounty Island (island south of New Zealand)

Brithysternum MacLeay, 1873
*__B. calcaratum__ MacLeay, 1873: Queensland (Australia)
**B. macleayi* Sloane, 1910: Northern Territory (Australia)
B. nodosum Sloane, 1910: Western Australia

Cascellius Curtis, 1839
*__C. gravesii__ Curtis, 1839: Austral *Nothofagus* forest in Argentina and Chile
= *Cascellius nitidus* Waterhouse, 1841 (taxonomic decision of Waterhouse, 1881)
= *Creobius troberti* Solier, 1849 (taxonomic decision of Fairmaire, 1885)
**C. septentrionalis* Roig-Juñent, 1995a: northern *Nothofagus* forest in Argentina and Chile

Cerotalis Castelnau, 1867
C. amabilis Sloane, 1890: West Plateau, NE coastal, and South Australia
C. brachypleura Sloane, 1898: Western Australia
C. longipes Sloane, 1898: Western Australia
C. majuscula (Putzeys, 1868) (as *Promecoderus*): Australia
C. semiviolacea Castelnau, 1867: South Australia and Victoria
*__C. substriata__ Castelnau, 1867 (present designation): Western Australia
C. versicolor Castelnau, 1867: Victoria (Australia)

Creobius Guérin-Méneville, 1838
*__C. eydouxii__ Guérin-Méneville, 1838: northern *Nothofagus* forest in Argentina and Chile
= *Cascellius kingii* Curtis, 1839 (taxonomic decision of Waterhouse, 1841b)
= *Creobius australis* Schweiger, 1959 (taxonomic decision of Roig-Juñent, 1995a)

Gnathoxys Westwood, 1842
G. barbatus MacLeay, 1864: South Australia
**G. cicatricosus* Reiche, 1842: Western Australia
G. crassipes Sloane, 1898: Western Australia
G. foveatus MacLeay, 1863-1866: Western Australia
*__G. granularis__ Westwood, 1842 (present designation as type species): Western Australia
= *G. blissii* MacLeay, 1866 (taxonomic decision of Csiki, 1928)
G. humeralis MacLeay, 1864: South Australia and Victoria
G. insignitus MacLeay, 1864: Western Australia
G. irregularis Westwood, 1842: Northern Territory (Australia)
G. macleayi Putzeys, 1868: Western Australia
G. murrumbidgensis MacLeay, 1865: New South Wales (Australia)
G. obscurus Reiche, 1842: Western Australia
G. punctipennis MacLeay, 1873: Western and South Australia
G. submetallicus MacLeay, 1864: South Australia
G. sulcicollis Sloane, 1910: Australia
**G. tesselatus* MacLeay, 1864: Victoria, New South Wales, and Queensland (Australia)
G. westwoodi Putzeys, 1868: Western Australia

Nothocascellius Roig-Juñent, 1995a
*__N. aeneoniger__ (Waterhouse, 1841) (as *Cascellius*): austral *Nothofagus* forest in Argentina and Chile
= *Cascellius niger* Blanchard, 1853 (taxonomic decision of Putzeys, 1868)
**N. hyadesii* (Fairmaire, 1885) (as *Cascellius*): moorland austral areas of Patagonia in Chile and Argentina

Promecoderus Dejean, 1829
**P. albaniensis* Castelnau, 1867: Australia, SW coastal zone
P. anguliceps Sloane, 1898: Western Australia
P. bassi Castelnau, 1867: Tasmania
P. blackburni Sloane, 1890: South Australia
*__P. brunnicornis__ Dejean, 1829: Tasmania
= *P. morosus* Putzeys, 1868 (taxonomic decision of Putzeys, 1873)
= *P. degener* Guérin-Méneville, 1841 (taxonomic decision of Sloane, 1920)
= *P. ovicollis* Castelnau, 1867, as a variety of *P. brunnicornis* by taxonomic decision of Sloane, 1920
P. castelnaui Sloane, 1892: New South Wales (Australia)
P. clivinoides Guérin-Méneville, 1841: NW and SW Australian coastal zone, Western Australia
= *P. minutus* Castelnau, 1867 (taxonomic decision of Putzeys, 1868)
**P. comes* Sloane, 1890: New South Wales (Australia)
**P. concolor* Germar, 1848: Adelaida (Australia)
= *P. suturalis* Castelnau, 1867 (taxonomic decision of Sloane, 1892)
= *P. howitti* Castelnau, 1867 (taxonomic decision of Sloane, 1892)

= *P. lucidus* Putzeys, 1868 (taxonomic decision of Sloane, 1892)
= *P. anthracinus* McLeay, 1873 (taxonomic decision of Sloane, 1892)
= *P. concolor namoyensis* Sloane, 1892 (taxonomic decision of Sloane, 1892)
= *P. lucidicollis* Castelnau, 1867 (taxonomic decision of Sloane, 1892)
= *P. politus* Sloane, 1890 (taxonomic decision of Sloane, 1892)
= *P. oblongus* Castelnau, 1867 (taxonomic decision of Sloane, 1892)
P. cordicollis Sloane, 1908: Tasmania
P. curvipes Sloane, 1920: Tasmania
P. distinctus Sloane, 1890: SW coastal, Western Australia
P. dorsalis MacLeay, 1873: Victoria and New South Wales (Australia)
**P. dyschiroides* Guérin-Méneville, 1841: NW coastal; SW coastal, Western Australia
P. elegans Castelnau, 1867: SE coastal and Victoria (Australia)
**P. gibbosus* (Gray, 1832) (as *Cnemacanthus*): Tasmania
P. hunteriensis MacLeay, 1873: SE coastal and New South Wales (Australia)
**P. inornatus* MacLeay, 1873: New South Wales (Australia)
= *P. puncticollis* MacLeay, 1873 (taxonomic decision of Sloane, 1890)
P. insignis Sloane, 1890: New South Wales (Australia)
P. intermedius Sloane, 1898: SW coastal and Western Australia
P. interruptus MacLeay, 1873: SE coastal and New South Wales (Australia)
P. leai Sloane, 1898: Western Australia
P. lottini Brullé, 1834: Type locality New Zealand. Lawrence et al., 1987, suppose that this is a locality error or this species has been placed in the wrong genus
P. maritimus Castelnau, 1867: SE coastal and Victoria (Australia)
P. mastersii MacLeay, 1873: SE coastal, Australian Capital Territory, and New South Wales (Australia)
P. modestus Castelanu, 1867: Tasmania
P. neglectus Castelnau, 1867: SE coastal, Victoria, and New South Wales (Australia)
= *P. puella* Putzeys, 1868 (taxonomic decision of Sloane, 1890)
P. nigellus Sloane, 1890: SE coastal and New South Wales (Australia)
P. nigricornis Castelnau, 1867: SE coastal and Victoria (Australia)
P. olivaceous MacLeay, 1873: SE coastal and New South Wales (Australia)
P. ovipennis Sloane, 1898: Western Australia and SW coastal
P. pacificus Sloane, 1890: Victoria (Australia)
P. pygmaeus Castelnau, 1867: Victoria (Australia)
P. riverinae MacLeay, 1873: New South Wales (Australia)
P. scauroides Castelnau, 1867: Western Australia
P. semistriatus Castelnau, 1867: New South Wales (Australia)
P. sloanei Blackburn, 1901: Western Australia
P. striatopunctatus Castelnau, 1867: New South Wales (Australia)
**P. subdepressus* Guérin-Méneville, 1841: Western Australia
P. viridiaeneus Sloane, 1915: Tasmania
P. wilcoxii Castelnau, 1867: New South Wales (Australia)

NOTHOBROSCINA

Brullea Castelnau, 1867
B. antarctica Castelnau, 1867: New Zealand, North Island and Auckland

Chylnus Sloane, 1920
***C. ater** (Putzeys, 1868) (as *Lychnus*): Tasmania
= *Lychnus strangulatus* Bates, 1878 (taxonomic decision of Sloane, 1892)
= *Lychnus striatulus* Bates, 1878 (taxonomic decision of Sloane, 1920)
**C. concolor* (Sloane, 1892) (as *Percosoma*) (new combination): Victoria (Australia)
C. montanum (Castelnau, 1867) (as *Mecodema*) (new combination): Victoria (Australia)
**C. substriatum* (Moore, 1960) (as *Percosoma*) (new combination): Victoria (Australia)

Dyglymma Sharp, 1886
D. castigatum Broun, 1909: Snares (south of New Zealand)
***D. clivinoides** (Castelnau, 1868); (as *Maoria*): New Zealand, South Island
= *Diglymma ovipenne* Sharp, 1886 (taxonomic decision of Britton, 1949)
= *D. dubium* Sharp, 1886 (taxonomic decision of Britton, 1949)
= *D. basale* Broun, 1917
D. marginale Broun, 1914: New Zealand, South Island
**D. obtusum* (Broun, 1893), (as *Metaglymma*): New Zealand, South Island
= *D. punctipenne* Broun, 1893 (taxonomic decision of Britton, 1949)
= *D. nigripes* Broun, 1893 (taxonomic decision of Britton, 1949)
= *D. tarsale* Broun, 1908 (taxonomic decision of Britton, 1949)

= *Snofru aemulator* Broun, 1908 (taxonomic decision of Britton, 1949)
= *D. thoracicum* Broun, 1917 (taxonomic decision of Britton, 1949)

Eurylychnus Bates, 1891
**E. blagravii* (Castelnau, 1868) (as *Mecodema*): Victoria (Australia)
= *Percosoma mastersi* Rainbow, 1899 (taxonomic decision of Moore, 1960)
**E. cylindricus* Sloane, 1916: New South Wales (Australia)
**E. dyschirioides* (Castelnau, 1868) (as *Maoria*): Victoria (Australia). The reference of New Zealand by Castelnau, 1868, is an error (Britton, 1949)
= **E. olliffi** Bates, 1891 (taxonomic decision of Sloane, 1911)
**E. femoralis* Sloane, 1915: Tasmania
E. kershawi Sloane, 1915: Victoria (Australia)
E. ovipennis Sloane, 1915: New South Wales (Australia)
**E. regularis* Sloane, 1911: Dorrigo (Australia)
E. victoriae Sloane, 1892: Victoria (Australia)

Mecodema Blanchard, 1853
M. allani Fairburn, 1945: New Zealand, South Island
M. alternans Castelnau, 1867: New Zealand, South Island, Chatham Islands
M. alternans hudsoni Broun, 1909, (changed status by Townsend, 1971): Snares (island south of New Zealand)
M. angustulum Broun, 1914: New Zealand, South Island
M. atrox Britton, 1949: New Zealand, North Island, Auckland
M. brittoni Townsend, 1965: New Zealand, South Island
M. bullatum Lewis, 1902: New Zealand, South Island
= *M. intricatum* Broun, 1903 (taxonomic decision of Britton, 1949)
M. chiltoni Broun, 1917: New Zealand, South Island
**M. costellum* Broun, 1903: New Zealand, South Island, Stephen's Island
M. costellum obesum Townsend, 1965: New Zealand, South Island
M. costellum gordonense Broun, 1917 (changed status by Townsend, 1965): New Zealand, South Island
M. costellum lewisi Broun, 1908 (changed status by Townsend, 1965): New Zealand, South Island
M. costipenne Broun, 1914: New Zealand, South Island
**M. crenaticolle* Redtenbacher, 1867: New Zealand, North Island
= *M. rugicolle* Broun, 1882 (taxonomic decision of Britton, 1949)
= *M. lineatum* Broun, 1894, (taxonomic decision of Lewis, 1902)
**M. crenicole* Castelnau, 1867: New Zealand, North Island, Auckland
= *M. venator* Broun, 1886 (taxonomic decision of Britton, 1949)
= *M. variolosum* Broun, 1903 (taxonomic decision of Britton, 1949)
=*M. attenuatum* Broun, 1908 (taxonomic decision of Britton, 1949)
= *M. ventriculum* Broun, 1923 (taxonomic decision of Britton, 1949)
M. curvidens (Broun, 1915) (as *Metaglymma*): New Zealand, North Island
M. ducale Sharp, 1886: New Zealand, South Island
M. dunense Townsend, 1965: New Zealand, South Island
M. dux Britton, 1949: New Zealand, North Island, Auckland
M. elongatum Castelnau, 1867: New Zealand, South Island
= *M. gratum* Broun, 1917 (taxonomic decision of Britton, 1949)
M. femorale Broun, 1921: New Zealand, South Island
= *M. veratrum* Broun, 1921 (taxonomic decision of Britton, 1949)
M. florae Britton, 1949: New Zealand, North and South Island
M. fulgidum Broun, 1881: New Zealand, South Island
= *M. halli* Broun, 1915 (taxonomic decision of Britton, 1949)
= *M. antennale* Broun, 1923 (taxonomic decision of Britton, 1949)
= *M. simulans* Hudson, 1934 (taxonomic decision of Britton, 1949)
= *M. constrictum* Broun, 1881 (taxonomic decision of Townsend, 1965)
= *M. cognatum* Broun, 1908 (as junior synonym of *M. constrictum*, taxonomic decision of Britton, 1949)
= *M. cassense* Broun, 1923 (as junior synonym of *M. constrictum*, taxonomic decision of Britton 1949)
M. gourlayi Britton, 1949: New Zealand
M. hector Britton, 1949: New Zealand, South Island
**M. howitti* Castelnau, 1867: New Zealand, South Island
M. huttense Broun, 1915: New Zealand, South Island
**M. impressum* Castelnau, 1867: New Zealand, South Island

= *M. mutabile* Broun, 1917 (taxonomic decision of Britton, 1949)
M. infimate Lewis, 1902: New Zealand, South Island
= *M. rubripes* Broun, 1917 (taxonomic decision of Britton, 1949)
M. integratum Townsend, 1965: New Zealand, South Island
M. laeviceps Broun, 1904: New Zealand, South Island
M. laterale Broun, 1917: New Zealand, South Island
M. litoreum Broun, 1886: New Zealand, South Island
= *M. dissonum* Broun, 1914 (taxonomic decision of Britton, 1949)
M. longicolle Broun, 1923: New Zealand, North Island
= *M. subaeneum* Broun, 1923 (taxonomic decision of Britton, 1949)
M. lucidum Castelnau, 1867: New Zealand, South Island
= *M. laevicolle* Broun, 1912 (taxonomic decision of Britton, 1949)
= *M. ambiguum* Broun, 1915 (taxonomic decision of Britton, 1949)
= *M. latulum* Broun, 1917 (taxonomic decision of Britton, 1949)
= *M. affinum* Broun, 1917 (taxonomic decision of Britton, 1949)
= *M. indiscretum* Broun, 1917 (taxonomic decision of Britton, 1949)
= *M. clarkei* Brookes, 1926 (taxonomic decision of Britton, 1949)
M. metallicum Sharp, 1886: New Zealand, South Island
M. minax Britton, 1949: New Zealand, South Island
M. morio (Castelnau, 1867) (as *Maoria*): New Zealand, South Island
= *Metaglymma punctifer* Broun, 1882 (taxonomic decision of Britton, 1949)
M. nitidum Broun, 1903: New Zealand, South Island
**M. oblongum* (Broun, 1882) (as *Metaglymma*): New Zealand, Cook Strait, North Island
= *M. insulare* Broun, 1921 (taxonomic decision of Britton, 1949)
M. occipitale Broun, 1923: New Zealand, North Island, Auckland
= *M. exitosum* Brookes, 1926 (taxonomic decision of Britton, 1949)
M. oconnori Broun, 1912: New Zealand, North Island
M. oregoide (Broun, 1894) (as *Metaglymma*): New Zealand, South Island
M. pavidum Townsend, 1965: New Zealand, South Island
M. pluto Britton, 1949: New Zealand, North Island, Auckland
M. politanum Broun, 1917: New Zealand, South Island
M. proximus Britton, 1949: New Zealand, South Island
M. pulchellum Townsend, 1965: New Zealand, South Island
M. punctatum Castelnau, 1867: New Zealand, South Island
= *M. aeneoniger* Broun, 1886 (taxonomic decision of Britton, 1949)
= *M. erraticum* Broun, 1917 (taxonomic decision of Britton, 1949)
M. punctellum Broun, 1921: New Zealand, South Island, Stephen's Island
M. quoinense Broun, 1912: New Zealand, North Island
**M. rectolineatum* Castelnau, 1867: New Zealand, South Island
= *M. suteri* Broun, 1893 (taxonomic decision of Britton, 1949)
M. regulus Britton, 1964: Three Kings Islands
M. rex Britton, 1949: New Zealand, South Island
M. rugiceps Sharp, 1886: New Zealand, South Island
= *M. seriatum* Broun, 1908 (taxonomic decision of Britton, 1949)
= *M. persculptum* Broun, 1915 (taxonomic decision of Townsend, 1965)
M. rugiceps anomalum Townsend, 1965: New Zealand, South Island
***M. sculpturatum** Blanchard, 1853: New Zealand, South Island
M. sculpturatum puncticolle Broun, 1914: New Zealand, South Island
M. simplex Castelnau, 1867: New Zealand, North Island, Auckland
= *M. acuductum* Broun, 1908 (taxonomic decision of Britton, 1949)
= *M. bryobium* Broun, 1912 (taxonomic decision of Britton, 1949)
= *M. arcuatum* Broum, 1912 (taxonomic decision of Britton, 1949)
M. spinifer Broun, 1880: New Zealand, North Island, Auckland
= *M. scitulum* Broun, 1894 (taxonomic decision of Britton, 1949)
M. striatum Broun, 1904: New Zealand, South Island
M. strictum Britton, 1949: New Zealand, South Island
M. sulcatum (Sharp, 1886) (as *Metaglymma*): New Zealand, North and South Island
= *Metaglymma modicum* Broun, 1894 (taxonomic decision of Britton, 1949)

= *Metaglymma douilli* Broun, 1905 (taxonomic decision of Britton, 1949)
= *Metaglymma ovicolle* Broun, 1914 (taxonomic decision of Britton, 1949)
M. trailli Broun, 1917: New Zealand, South Island
= *M. philpotti* Broun, 1923 (taxonomic decision of Britton, 1949)
M. validum Broun, 1923: New Zealand, North Island

Metaglymma Bates, 1867
**M. aberrans* Putzeys, 1868: New Zealand, South Island
= *M. tersatum* Broun, 1893 (taxonomic decision of Britton, 1949)
= *M. thoracicum* Broun, 1893 (taxonomic decision of Britton, 1949)
= *M. rugiceps* Broun, 1903 (taxonomic decision of Britton, 1949)
****M. moniliforme** Bates, 1867: New Zealand, South Island
= *M. rugipenne* Broun, 1893 (taxonomic decision of Britton, 1949)
= *M. minor* Broun, 1905 (taxonomic decision of Britton, 1949)
**M. tibiale* (Castelnau, 1867) (as *Maoria*); New Zealand, South Island
= *Mecodema ruficeps* Broun, 1886 (taxonomic decision of Britton, 1949)
= *Mecodema asperum* Broun, 1893 (taxonomic decision of Britton, 1949)
= *Mecodema junctum* Broun, 1893 (taxonomic decision of Britton, 1949)
= *Mecodema calcaratum* Broun, 1903 (taxonomic decision of Britton, 1949)

Nothobroscus Roig-Juñent and Ball, 1995
****N. chilensis** Roig-Juñent and Ball, 1995: northern *Nothofagus* forest of Chile

Oregus Putzeys, 1868
****O. aereus** (White, 1846) (as *Promecoderus*): New Zealand, South Island
**O. inaequalis* (Castelnau, 1867) (as *Mecodema*): New Zealand, South Island

Percolestus Sloane, 1892
****P. blackburni** Sloane, 1892: Victoria (Australia)

Percosoma Schaum, 1858
P. asymetricum Fauvel, 1903: New Caledonia.
****P. carenoides** (White, 1846) (as *Broscus*): Tasmania
= *Broscus hopei* Sturm, 1843 [nomen nudum]
= *Mecodema percoides* Castelnau, 1867 (taxonomic decision of Putzeys, 1868)
**P. sulcipenne* Bates, 1878: Tasmania

INCERTAE SEDIS
Ebertius Jedlička, 1965
E. nepalensis Jedlička, 1965: Nepal

APPENDIX 2

Abbreviations used in figures

acg	accessory gland
ae	lateroapical projections of sclerite X
ao	apical orifice; apapical plate
ap	apical plate
bk	basal keel
bo	basal orifice
c	central constriction of sclerite X
ep	elytral plica
hs	helmintoid sclerite
p	spiculae of apical plate fused forming a plate
r	row of posterolateral setae of antennomere 2–5
sbr	suborbital ridge
sp	spermatheca
sz	subocular zone
t	central tooth of apical plate
th	tooth of the apical plate
tr	temporal ridge
vap	vaginal apophysis
X	sclerite X
Y	sclerite Y